

TRANSACTIONS  
OF  
THE ZOOLOGICAL SOCIETY  
OF LONDON.

VOLUME XXVI.

---

LONDON:

PRINTED FOR THE SOCIETY:

SOLD AT THEIR HOUSE IN REGENT'S PARK;  
AND BY MESSRS. LONGMANS, GREEN, AND CO., LTD.,  
6 & 7 CLIFFORD STREET, LONDON, W. 1.

---

1947-1950.

PRINTED BY TAYLOR & FRANCIS, LTD.,  
RED LION COURT, FLEET STREET, E.C.4.



# ALPHABETICAL LIST

## OF THE

## CONTRIBUTORS.

---

	Page
<b>DE BEER, G. R.</b> <i>See</i> <b>HILL, J. P.</b>	
<b>FLYNN, T. THOMSON.</b>	
Description of <i>Prosqualodon davidi</i> Flynn, a Fossil Cetacean from Tasmania. (Plates I-VI; Text-figures 1-11.)	153
(Published August, 1948.)	
<b>FLYNN, T. THOMSON, and HILL, J. P.</b>	
The Development of the Monotremata.—Part VI. The Later Stages of Cleavage and the Formation of the Primary Germ-layers. (Plates I-XXVII.)	1
(Published July, 1947.)	
<b>HILL, J. P., and DE BEER, G. R.</b>	
Development of the Monotremata.—Part VII. The Development and Structure of the Egg-tooth and the Caruncle in the Monotremes and on the Occurrence of Vestiges of the Egg-tooth and Caruncle in Marsupials. (Plates I-X.)	503
(Published March, 1950.)	
<b>HILL, J. P.</b> <i>See</i> <b>FLYNN, T. THOMSON.</b>	
<b>HILL, W. C. OSMAN, and REWELL, R. E.</b>	
The Caecum of Primates.—Its Appendages, Mesenteries and Blood Supply. (Plates I-VI.)	199
(Published December, 1948.)	
<b>HULL, FRANK M.</b>	
The Morphology and Inter-relationship of the Genera of Syrphid Flies, Recent and Fossil. (Text-figures 1-25.)	257
(Published May, 1949.)	
<b>JONES, FREDERIC WOOD.</b>	
The Study of a Generalized Marsupial ( <i>Dasyercus cristicauda</i> Krefft). (Plates I & II; Text-figures 1-99.)	409
(Published November, 1949.)	
<b>REWELL, R. E.</b> <i>See</i> <b>HILL, W. C. OSMAN.</b>	





# TRANSACTIONS

OF

## THE ZOOLOGICAL SOCIETY

## OF LONDON.

*The Development of the Monotremata.*—Part VI. *The Later Stages of Cleavage and the Formation of the Primary Germ-layers.* By Professor T. THOMSON FLYNN, M.B.E., D.Sc., and Professor J. P. HILL, F.R.S., F.Z.S.

(PLATES I-XXVII.)

[Received October 23rd, 1945.]

### TABLE OF CONTENTS.

	Page
INTRODUCTION .....	2
SYNOPSIS, GROUPS I-V .....	3
SYSTEMATIC DESCRIPTION OF MATERIAL .....	5
Group I .....	5
SUMMARY AND DISCUSSION OF LATER CLEAVAGE STAGES (LC 1-7) .....	29
Group II .....	33
Group III .....	44
Group IV .....	68
Group V .....	75
FINAL SUMMARY AND DISCUSSION .....	102
A. Formation and Growth of the Blastoderm .....	102
1. The Germ-ring .....	102
2. Transformation of the Blastodisc into the Blastoderm .....	104
3. The Marginal Region of the Sauropsidan Blastoderm and the Homology of the Germ-ring .....	105
4. The Yolk-navel in the Reptilia in comparison with that of the Monotremata .....	110
5. The Yolk-bed: Yolk-bed Cells and Nuclei .....	111
B. Formation of the Primary Germ-layers .....	114
1. The Constitution of the Blastoderm .....	114
2. First Phase: Formation of the Unilaminar Blastoderm .....	115
3. Second Phase: Formation of the Bilaminar Blastoderm .....	117
C. The Early Development of the Sub-classes of the Mammalia .....	120
D. The Origin of the Primary Germ-layers in the Sauropsida .....	126
1. Reptiles .....	126
2. Birds, by J. H. Woodger and J. P. Hill .....	128
LITERATURE CITED .....	132
EXPLANATION OF PLATES .....	136



## INTRODUCTION.

In Part IV of this series of contributions to our knowledge of the development of the Monotremes (Flynn and Hill, 1939), we gave an account of the meroblastic cleavage process in the egg, up to the stage when the blastodisc is composed of 32 blastomeres or cleavage cell-areas forming a single layer and all of them in open continuity below with the underlying yolk.

In the present part, of which a summary has been published in the Proceedings of the Society (ser. A, vol. 111, 1941), we provide first of all a description of the later stages of cleavage which are available in our collection, up to the establishment of the blastodisc as a small biconvex lens-shaped mass, some four cells in thickness centrally, and occupying a slight depression, floored by the yolk-bed, at the upper pole of the egg. Then we pass to describe successively the later history of the blastodisc, its transformation, consequent on the formation of the germ-ring, into a blastoderm, capable of growing so as to enclose the yolk-mass of the egg, and lastly, the formation of the two primary germ-layers as the result of the segregation of the two categories of cells which become distinguishable in the blastoderm, into two distinct layers, respectively superficial and deep.

The material at our disposal for this part of our work comprises well over 40 eggs of *Echidna* (of which 37 have been utilized in the preparation of this communication), together with two pairs of twin-eggs of *Ornithorhynchus*. This material we have been able to arrange in five well-defined groups which represent successive phases in ontogenesis. It has enabled us to provide for the first time what we think is a reasonably complete and well-authenticated account of the mode of formation of the primary germ-layers in this the most primitive order of the Mammalia.

We are again greatly indebted to Miss F. M. Collinson for the care and skill she has displayed in the preparation of the illustrations, the great majority of which are from her hand. For the remainder we have to thank Mr. A. K. Maxwell. To Mr. F. J. Pittock, F.R.P.S., of the Department of Anatomy, University College, London, we tender our grateful thanks for the generous and unstinted help he has again given us in providing the photo-micrographs on which the illustrations are based. We also desire to offer our very cordial thanks to Dr. Una Fielding, Acting Head of the Department, and to Mr. K. C. Richardson, Reader in Histology, for granting us the necessary facilities, and for their generous hospitality during visits to Leatherhead, where the Department was located during the war-years. For technical assistance, we are much indebted to Mr. H. Barker.

The serial sections of the eggs and many of the illustrations, fortunately enough, were prepared prior to the outbreak of hostilities in September 1939, and preliminary observations on the late cleavage stages had been made, so that, in spite of the hazards of war and the lack of proper laboratory facilities, it has been possible to carry on with, and to complete to the best of our ability, the study of the unique material in our possession. It should be stated, however, that owing to war-time conditions and the appointment of one of us (F.) as Chief Casualty Officer to the Civil Defence Authority, Belfast, the completion of the text has largely devolved on the other author (H.). In carrying out this task he desires to acknowledge with deep gratitude the very material and generous



aid he has received from the Trustees of the Sir Halley Stewart Trust by their award to him of a Sir Halley Stewart Fellowship.

We also desire to express our grateful thanks to the Council of the Royal Society for a grant to enable us to complete the remaining illustrations.

#### SYNOPSIS.—GROUPS I-V.

Even at the risk of some repetition, it may serve a useful purpose if we present here a brief outline of the outstanding features in the ontogenesis of the primary germ-layers as seen in our Groups I-V.

Group I includes the initial stages in the meroblastic cleavage process up to the 32-celled stage (CG), previously described in Part IV (pp. 555-577), together with the seven later stages (LC 1-7) herein dealt with, up to the establishment of the biconvex lens-shaped blastodisc, with a diameter of about 0.50 mm. and some four cells thick centrally where it reaches a maximum thickness of about 0.080 mm. The disc is already well delimited from the yolk-bed on which it rests, except in its peripheral region, where some of the cells still remain open to the yolk, and where occasional gaps occur in the yolk-membrane through which yolk-spheres would seem to gain access to the disc. In the marginal zone of the yolk-bed, around and below the periphery of the disc, there are present numbers of highly characteristic free cells possessed of the power of migration, which we have termed "vitellocytes." They are formed by the division of the marginal cells of the disc, and have already appeared in the earliest of our later cleavage stages (LC 1). In addition, in two stages (LC 4 and 5), free cells (sub-disc cells) also occur in the yolk-bed below the disc. These two varieties of cells are comparable with the yolk-cells or merocytes which occur in the yolk below and around the blastodisc in the Reptilian egg.

Group II marks the culmination of the cleavage process and the attainment by the blastodisc of its completed condition. Its members exhibit a steady progressive increase in the number of their constituent blastomeres as we pass from the earliest (VVH 36) to the most advanced stage in the Group (VVH 41), but, remarkably enough, this increase in number is not marked by a decrease in the size of the cells; on the contrary, it is in this Group that the blastomeres, consequent on their active assimilation of yolk, attain their maximum size, and the blastodisc its maximum thickness (0.16 mm. in VVH 17). But it is to be noted that, whilst the blastodiscs in this Group are definitely thicker than those of Group I, they show no significant increase in diameter over those of the latter, the largest blastodisc in the Group, that of VVH 41, possessing a diameter of  $0.55 \times 0.50$  mm. as compared with the largest in Group I, LC 7, with a diameter of  $0.55 \times 0.51$  mm.

Group III is of special interest and importance, since three events of prime developmental significance occur within its limits. These are as follows:—(1) The vitellocytes, which have in the meantime increased in number and size, fuse together to form a continuous nucleated syncytial ring which encircles the periphery of the blastodisc, and to the surface of which the peripheral cells of the latter become attached. This we have termed the "germ-ring." Like its parent vitellocytes it is endowed with the capacity of migration. (2) As soon as the germ-ring is fully established it begins to migrate outwards over the yolk, and the



connection of the peripheral cells with its surface somehow or other induces the blastodisc to follow suit. The blastodisc accordingly increases in surface-extent, and at the same time it undergoes a reduction in its thickness. As the outcome the originally compact thick disc gradually becomes transformed into a relatively thin blastoderm, composed of a superficial layer, with below it more or less dispersed deep cells, and some two to three cells in thickness centrally. The blastoderm so constituted and preceded by the germ-ring continues to progress peripherally over the surface of the yolk-mass of the egg, and already in the latest member of the Group (VVH 6) has attained a diameter of  $1.36 \times 1.38$  mm., as compared with a diameter of 0.56 mm. in the youngest member (VVH 35), whilst its thickness has become reduced from 0.136 mm. in the latter to about 0.032 mm. (3) In the most advanced members of the Group, the constituent cells of the blastoderm have become distinguishable by their cytological characters into two well-defined categories, viz.: (a) prospective ectodermal cells, and (b) primitive endoderm cells.

Group IV.—In the interval between this Group and the preceding the blastoderm has more than doubled its diameter, and during this growth a remarkable change has taken place, since all its deeply situated cells have crowded up into the superficial layer. The blastoderm has thus become transformed into a thin unilaminar membrane. The attainment of this condition constitutes the first step in germ-layer formation, since it ensures that all the prospective ectodermal cells have been brought into their definitive position at the surface. The second step involves the acquisition by the primitive endoderm cells of their final deep position below the superficial layer formed by the ectodermal cells, and this they effect mainly by a process of active inward migration.

Group V.—In the members of this last Group we observe two significant events: (a) the progressive enclosure of the yolk-mass of the egg by the spreading blastoderm, the final point of closure being marked by a cicatricial thickening, the yolk-navel, at the lower pole, and (b) the gradual migration of the primitive endoderm cells to their definitive deep position below the ectodermal cells which remain passively at the surface. The primitive endoderm cells are endowed with amoeboid properties, and are capable of effecting migratory movements and of sending out pseudopodial processes as well before, but especially after, their migration out of the unilaminar blastodermic membrane. They also divide actively whilst still intercalated in the latter, as well as after their migration, and so increase greatly in number. The pseudopodial processes they produce anastomose with those of other cells or directly with their cell-bodies, thus producing irregular cell-networks. Out of these and the occasional cell-groups and isolated cells which occur interspersed amongst the latter, a continuous layer of endoderm is gradually differentiated, whilst the superficially situated ectodermal cells constitute a layer of flattened ectoderm.

The primary germ-layers accordingly owe their origin to the segregation of the cells belonging to the two categories which first become clearly distinguishable in the later members of Group III, into the two distinct layers which constitute the bilaminar blastoderm, viz., a superficial layer of ectoderm and a deep layer of endoderm. The cells of the latter sooner or later proceed to engulf large yolk-spheres, and in this way the endoderm acquires secondarily the characters of a genuine yolk-endoderm.



## SYSTEMATIC DESCRIPTION OF MATERIAL.

## GROUP I.

In this first Group we include the initial stages in the meroblastic cleavage process up to the 32-celled stage (CG), which we have previously described, and the immediately succeeding later cleavage stages, numbering nine in our collection, of which seven, designated LC 1-7, are deserving of detailed description.

It may be recalled that at the 31- and 32-celled stages (CF and CG) the blastodisc consists of a single layer of "blastomeres" or cleavage cell-areas, as the cleavage-products are more correctly designated at this period, since all of them are still in open continuity with the yolk-bed, though with this proviso in mind we may, for convenience, continue to speak of them as cells or blastomeres. They exhibit a highly characteristic arrangement into two groups, viz.: an outer ring of larger "marginal" blastomeres separated from each other by radial furrows and in continuity with the fine-grained marginal zone of the yolk-bed at their peripheral ends as well as below, and an inner group of smaller "central" blastomeres, delimited from each other by vertical furrows and in open continuity with the yolk-bed below.

The same arrangement of the blastomeres into marginal and central can still be detected in the earlier blastodiscs here dealt with, but already in LC 3 the marginals have all been used up in furnishing their products, and are no longer recognizable as such.

In these later blastodiscs, as we pass from the earliest to the most advanced member of the series, we observe a progressive increase in the number of their constituent blastomeres as the result of active mitotic division. The divisions are effected not only in planes vertical to the surface but also in planes horizontal or oblique thereto, with the result that the disc becomes more than one cell thick, and with the continuance of such division eventually attains a thickness of about four cells in its central region.

We can thus draw a distinction between superficially situated and deep cells. Furthermore, as cleavage proceeds, the most deeply situated cells in the central region, which for a time remain open to the yolk, progressively round themselves off and become completely delimited from the latter. The end-result, as seen in LC 6 and 7, is the formation of a circular biconvex blastodisc, resting in a slight depression at the upper pole of the egg, floored by the yolk-bed, from which it is sharply delimited, except in its peripheral region. It is about four cells in thickness centrally and thins out gradually to the thickness of a single cell at its periphery. The disc so constituted has a diameter of just over 0.5 mm. and a maximum thickness centrally of about 0.08 mm.

One of the most striking features of this developmental period is the very early appearance (already in LC 1) in the superficial yolk of the marginal zone around the periphery of the disc, of relatively numerous cells of a quite remarkable character. They possess more or less flattened cell-bodies of irregular outline, the cytoplasm of which is produced peripherally and below into thin tapering processes of varying length, suggestive of pseudopodia. These processes frequently anastomose with each other as well as with those of adjacent cells, and extending out between and around the yolk-spheres abutting on the cell-body, they can be



traced into direct continuity with the delicate cytoplasmic reticulum which pervades the yolk-bed including the marginal zone, and in whose meshes the yolk-spheres are situated.

In addition to the large and small spheres more or less completely enclosed by the processes in vacuolar-like spaces, fine yolk-spheres are generally present in the cytoplasm of the upper half of the cell-body, being especially numerous in cells recently formed.

The cells lie at first adjacent to the periphery of the disc, close below or actually in contact with the egg- or yolk-membrane, but remarkably enough, they are endowed with the capacity for migration, and whilst some of them remain in the position mentioned others wander out in contact with the egg-membrane, for varying, often quite considerable, distances from the disc-margin. Yet others penetrate more deeply into the yolk, whilst still others migrate inwards, usually in contact with the yolk-membrane below the periphery of the disc, and so come to occupy a sub-marginal as contrasted with a peripheral position.

The evidence shows that they are derived from the marginal cells of the disc, and that they increase in number by division. In how far they are comparable with or related to the elements in the Sauropsidan germ variously known as "merocytes," yolk-cells or "periblast" may be left for subsequent discussion (*vide*, p. 30). Meantime, as none of these terms seems appropriate for the cells with which we are here concerned, we propose to speak of them as "vitellocytes," not, perhaps, a very satisfactory designation from the point of view of their significance, though it does at least indicate that they are in some way related to the yolk. The prime importance of these cells lies in the fact that in much later stages belonging to Group III, they fuse together to form a continuous ring of nucleated cytoplasm, a veritable marginal syncytium which encircles the blastodisc, and to whose surface the peripheral cells of the latter become attached. This syncytial formation plays an all-important part in the development of the egg. Retaining the migratory capacity of its progenitors, it initiates and conditions the increase in the surface-extent of the blastodisc and its conversion into a blastoderm as well as the continued peripheral growth of the latter, until it finally effects the complete enclosure of the yolk-mass of the egg.

In our preliminary communication (1941), we employed the term "germ-wall" to designate this syncytial formation, a somewhat unfortunate choice, as we now realize, since certain recent writers on the early development of Reptiles and Birds (*e. g.*, Will (1895) and Peter (1938)), have used this term ("Keimwall") to designate the undifferentiated ring of cells forming the marginal zone of the blastodisc or blastoderm, in which no distinction into layers is recognizable. For example, Peter (1938), in a recent paper on the origin of the endoderm in Reptiles, in describing the early blastodisc of *Lacerta* states "der Keimwall bildet den Rand der Keimscheibe. Er ist dick und besteht aus eng aneinander gepressten Zellen" (p. 502), whilst, with reference to the blastodisc of the pigeon, the same author (1938 (2)) affirms *contra* Patterson (1909, p. 78), "dass der Keimwall weder ein Syncytium darstellt, noch in irgendeinem Stadium mit dem Dotter in Verbindung steht" (p. 430). Similarly, Will (1895) in his paper on the development of *Lacerta* writes "Der Keimwall bildet die Randzone der ganzen Keimscheibe und ist je nach dem Alter der Keimscheibe von verschiedener Dicke, in dem



vorliegenden Stadium an der dicksten Stelle etwa 6-8 Zellen stark, um gegen den Keimscheibenrand keilartig auszulaufen " (p. 14).

It is to be noted, however, that the "Keimwall" of these two investigators appears to be quite distinct from the formation to which His (1868) originally applied the name of "Keimwall" in the blastoderm of the Fowl. This same formation Goette (1874) termed the "Randwulst," Kölliker (1875), the "Keimwulst," Balfour (1881), the "germinal wall," and Duval (1884), the "bourrelet blastodermique." There has been much controversy as to its structure and relations, arising partly from inherent difficulties of observation and interpretation, partly because its early history was quite unknown to the older workers. We now know from the work of Blount (1907), on the egg of the Pigeon, that it originates from the nucleated zone of cytoplasm which surrounds and underlies the blastodisc, and for which she has adopted the term "periblast" (*vide*, p. 107). The nuclei present in it are furnished, according to the authoress, by the division of the nuclei of the marginal cells of the blastodisc.

If these conclusions of Blount's are accepted, then it is clear that the syncytial ring in the Monotreme egg, to which we applied the term "germ-wall," is not comparable developmentally with the structure originally so named by His in the egg of the Fowl, nor is it in any way comparable with the so-called "Keimwall" of Peter and Will. Accordingly, to avoid further confusion, we propose to designate it henceforth as the "germ-ring," or alternatively as the "syncytial ring." But for its length, an even more appropriate designation would be "marginal syncytium." Unlike the periblast of Blount which only secondarily becomes permeated by nuclei, the Monotreme germ-ring is a true syncytium, formed by the fusion of cells (vitellocytes).

Whether the vitellocytes, whilst still isolated, play any subsidiary rôle in development, apart from enclosing yolk-spheres, we are unable to say. But in view of the occurrence in Reptilian eggs, of the process of "Nachfurchung" so-called, in connection with "merocytes" or yolk-nuclei" (*cf.* Virchow, 1892 *b*, Will, 1895, and others), and of statements (*cf.* Blount (1907)) to the effect that in birds, the central and marginal periblast actively contribute cells to the blastodisc and blastoderm, and in view also of certain appearances in our own sections, we have carefully considered the possibility that some of the vitellocytes (more particularly sub-marginals) might become included in the peripheral region of the blastodisc during the later stages of cleavage. We are satisfied, however, that if this happens at all it is a rare, and more or less accidental, occurrence of no general significance. The germ-ring certainly makes no cellular contribution to the blastoderm.

We now pass to the detailed description of the later cleavage stages (LC 1-7) included in the Group. It should be remarked that all the blastodiscs here dealt with, except one, were sectioned before we had perfected our technique, the blastodiscs, together with the immediately adjoining yolk, having been isolated from the remainder of the yolk-mass, prior to imbedding. In spite of this rather drastic procedure, the blastodiscs suffered no very extensive damage, and the serial sections are reasonably good, though it must be admitted they are not up to the standard of those prepared later, either as regards staining or completeness. As a consequence, their interpretation has proved both difficult and laborious,



and such description of them as we are able to provide is, we feel, far from constituting an adequate account of this important phase of development. For that a much larger number of blastodiscs is necessary than the few available to us. In those cases (LC 1-4) where we have attempted an enumeration of the cells the numbers given must be regarded as approximate only.

LC 1 (E.1.8.30). (Pl. I, figs. 1-4, 5 *a*, *b*, *c*.)

(Diameter of egg 4.0 mm. (fresh), 4.4 mm. (in alcohol). Diameter of blastodisc (from the sections)  $0.47 \times 0.512$  mm. Thickness, mostly 0.024-0.028 mm. Shell, 0.0062 mm. in thickness. Fixation, Bouin's Fluid.)

This blastodisc, which follows on the 31- and 32-celled stages (CF and CG) described in Part IV, is formed, so far as we can determine, of about 41 actual or potential cells, and though the increase in the number of blastomeres is but slight it exhibits a very definite advance on CF and CG inasmuch as deep cells are now in process of formation and vitellocytes have already appeared. The disc, however, has the same general constitution as in these, *i. e.*, it consists of a group of smaller central blastomeres and a surrounding series of larger marginal blastomeres, but whereas the centrals have increased from 17 in CG to 27, the marginals have become reduced from 15 to 10. The increase in the number of central cells may be effected in two ways: (*a*) by the division in the vertical plane of pre-existing centrals, (*b*) as the result of the tangential division of a marginal into an inner cell, which forms a central and an outer cell which may eventually become converted into a peripheral disc-cell or a vitellocyte. The marginal cells are gradually used up in the production of central and peripheral disc-cells and vitellocytes, and by the time we reach LC 3 are no longer recognizable as such. Pl. I, fig. 1 illustrates a section just to one side of the centre of the disc. It should be compared with Pl. XIX, fig. 105 and Pl. XX, fig. 109 of Part IV, illustrating sections through the discs of stages CF and CG. Making allowance for the fact that these latter eggs were fixed in Smith's Fluid (FBA), which tends to exaggerate the cleavage furrows, whereas the present egg was fixed in Bouin's Fluid, which seems to have the opposite effect, it will be seen that the central cells have now a much more flattened form than those of CF and CG, and lie in much closer apposition with each other, the only conspicuous cleavage furrows being those separating the marginal cells at the periphery of the disc from the group of central cells, though in sections more peripherally situated we do meet with central cells separated by definite furrows.

All the central cells except two are still in broad continuity below with the underlying coarsely vacuolated and fine-grained yolk-bed. One of the two is an ovalish cell ( $0.060 \times 0.024$  mm. in diameter) with clear homogeneous cytoplasm, devoid of yolk which is completely isolated, its peripheral region appearing in the section illustrated in Pl. I, fig. 2 (*c*. 1). The other is seen in Pl. I, fig. 3 (*c*. 2), and in this section appears isolated. Actually it is in continuity with the yolk-bed over a very limited area in the region of the vacuolated patch containing fine yolk-granules, which is visible in the figure close to the lower border of the cell.

This complete, or all but complete, separation or delimitation of the blastomeres from the yolk-bed is clearly not the result of cell-division in the horizontal plane, since no underlying cells or nuclei are present, but is due to a spontaneous rounding

off or separation of the cytoplasm of the blastomeres from the cytoplasmic reticulum of the yolk-bed, with accompanying formation of limiting cell-membranes.

The central cells range in diameter from  $0.033 \times 0.018$  mm. (nucleus  $0.009 \times 0.005$  mm.) to  $0.084 \times 0.027$  mm. (nucleus,  $0.012 \times 0.006$  mm.). The average diameter in ten cells measured is  $0.063 \times 0.021$  mm., that of their nuclei  $0.010 \times 0.005$  mm.

In the central region of the disc the cytoplasm of the cells therein situated is mostly homogeneous and uniformly light-staining, but in some of the cells, especially in the peripheral region of the disc, the cytoplasm of their upper halves stains much more deeply than the remainder. Some, at least, of the cells of this type in the peripheral region have been derived from marginals. The nuclei are oval, flattened, and horizontally disposed, and appear small relatively to the cell-body.

Altogether in this disc we estimate there are about 27 actual or potential central cells. Of these, 13 are separated by vertical furrows and are uninucleate (one of them, referred to above, being delimited from the yolk-bed and a second in process of becoming so); two are in process of division, forming two pairs of sister-cells, the members of each pair being still connected, but with more or less marked, though incomplete vertical cleavage furrows between them; two are still in continuity with their parent marginals, superficial tangential grooves marking the planes of their eventual separation; lastly there are four paired blastomeres (four pairs of daughter-cells in which division of the cytoplasm has not yet been completed) which are deserving of more detailed notice. Two of them are illustrated in Pl. I, figs. 1 (*c. 5* and *c. 6*) and 2 (*c. 3* and *c. 4*).

In all four the parent cell had evidently assumed an obliquely rhomboidal form, and when its nucleus divided in an obliquely horizontal plane the deeper of the two daughter-nuclei, in conformity with the plane of division and the shape of the cell, occupied a position not directly below the upper one, but to one side of it, so that a line joining the two is oblique to the surface (Pl. I, fig. 2, *c. 3* and *c. 4*). Division of the cytoplasm has been initiated by the appearance of a constriction or groove passing obliquely round the body of the cell, but situated nearer to the lower nucleus. Its completion would accordingly result in the formation of a larger superficial cell and a smaller deep cell, situated obliquely below its sister-cell. The division is clearly an unequal one, and one outcome of the obliquity of its plane is that both daughter-cells remain temporarily in continuity with the yolk-bed.

The most advanced member of the four is illustrated in Pl. I, fig. 2. In that figure a large superficially situated cell (*c. 3*) is seen to be in continuity by a narrow neck with a smaller deep cell (*c. 4*) lying obliquely below it. The superficial cell has a long diameter of 0.060 mm. and a thickness of about 0.018 mm., whilst its nucleus has a diameter of  $0.012 \times 0.006$  mm. The corresponding measurements of the deep cell are  $0.039 \times 0.021$  mm., nucleus  $0.0097 \times 0.006$  mm. Both daughter-cells, it will be noticed, are in open continuity with the yolk-bed. The other three members (one of them appears in Pl. I, fig. 1 (*c. 5* and *c. 6*)) are very similar to the foregoing, but the oblique groove marking the plane of division is much less marked, and the difference in size of the two daughter-cells is not always so accentuated as in it.



The interest of these particular blastomeres is that they show us the initial step in the formation of deep cells, and consequently in the transformation of the one-layered disc into a stratified disc, several cells in thickness.

*Marginal blastomeres.*—As in eggs CF and CG, the marginal cells are characterized by their peripheral position, large size, and flattened form, by their continuity with the yolk of the marginal zone below and at their outer margins, and by the presence of fine yolk-spheres or granules in their superficial cytoplasm, and of coarser spheres in their marginal, and sometimes also in their deep cytoplasm.

We estimate there are ten marginal cells in the present stage, a reduction of five as compared with CG. Of these: three are uninucleate and of the normal type; three are binucleate, one being devoid of any indication of cytoplasmic division, the other two possessing superficial radial grooves marking them out into daughter-cells, possibly destined to form peripheral disc-cells; two are in process of division into a larger peripheral cell and a smaller central, a tangential groove marking the plane of separation (Pl. I, fig. 3, *pdc.* and *cc.*); the remaining two are in continuity at their outer margins with peripherally situated cells which have the characters of vitellocytes, and so are deserving of brief description. One of the two is a large cell, measuring  $0.080 \times 0.024$  mm. in diameter, the cytoplasm of which in its upper three-quarters has stained more deeply than that of the remaining quarter. It contains sparse fine yolk-granules below its upper surface, and small yolk-spheres in its marginal region. At its outer end it passes into continuity with a cell which we regard as a prospective vitellocyte, a superficial groove marking the junction of the two. This cell is flattened like its sister-cell, and slightly smaller, measuring about  $0.072 \times 0.026$  mm. in diameter. Its cytoplasm has stained deeply throughout, and contains sparse fine yolk-granules below its upper surface. Its lower surface presents a ragged uneven contour owing to the presence of short anastomosing processes which are beginning to enclose underlying yolk-spheres of the marginal zone.

The second of the two marginals (Pl. I, fig. 5 *a*, *mc.*) is very similar to the one just described, but is larger, its diameter being  $0.108 \times 0.021$  mm., and that of its nucleus  $0.013 \times 0.005$  mm. The cytoplasm of its upper half only has stained deeply, and contains fine yolk-granules and sparse small yolk-spheres below its upper surface, as well as small spheres of varying size in its marginal region. At its outer end (Pl. I, fig. 5 *a*, on the right) it is continuous by way of a constricted neck with a prospective vitellocyte (Pl. I, fig. 5 *a*, *b*, and *c*, *pv.*), rather less advanced than that above described, and somewhat smaller than its sister-cell, its diameter being  $0.075 \times 0.021$  mm., and that of its nucleus  $0.013 \times 0.006$  mm. It differs from the latter in that its cytoplasm stains deeply throughout, and in its somewhat richer yolk-content, minute yolk-granules, and small spheres being present in its superficial and marginal cytoplasm, whilst larger spheres are becoming enclosed by the anastomosing processes which arise from its under-surface and periphery (Pl. I, fig. 5 *b* and *c*, *pv.*).

It would appear, then, that in both these cases the parent marginal cell has all but completely divided into two daughter-cells, one (proximal) retaining the characters of the parent marginal, the other (distal) in process of acquiring the characters of a vitellocyte.



*Vitellocytes*.—The fact noted above that these remarkable cells have already made their appearance in this relatively early stage is of no little interest in view of the all-important rôle they are destined to play in the development of the egg.

About twenty-two are already present, and of these twelve are uninucleate and isolated, eight are in continuity in pairs, whilst two are still in continuity as above described with their parent marginals.

The isolated vitellocytes, of which a fairly typical example is seen in Pl. I, fig. 4, take the form of rather flattened cells of highly characteristic appearance. The upper surface of the cell is smooth and even, but its under-surface and periphery are quite irregular, and lack a definite contour owing to the presence of fine cytoplasmic processes which arise therefrom, and are devoid of any regularity in their disposition. The cells lie adjacent to the peripheral cells of the disc (in one case 0.12 mm. distant from the nearest marginal cell), and are situated quite superficially in the yolk of the marginal zone, their upper surfaces (clothed by the egg-membrane) lying in close contact with the under-surface of the zona-albumen layer. They range in long diameter from about 0.060 to 0.10 mm. (but are difficult to measure accurately), and in thickness up to a maximum of about 0.020 mm. Their nuclei, mostly appearing rather elongated and flattened, vary in diameter from about  $0.009 \times 0.004$  mm. to  $0.012 \times 0.006$  mm. The greater part of the cell-body is formed of homogeneous, very finely granular cytoplasm, which usually stains uniformly. But below the upper surface is a narrow zone of cytoplasm in which are situated more or less numerous fine yolk-granules of varying size, and sometimes also small yolk-spheres, and such may also be present in the peripheral cytoplasm (Pl. I, fig. 4). The cytoplasmic processes above mentioned, which arise from the under-surface and periphery of the cell-body, constitute a very distinctive feature of these cells. They appear as delicate tapering outgrowths, mostly still quite short, and often containing minute yolk-granules. They usually occur singly, though they sometimes anastomose with each other. They extend down into the adjoining yolk and between some of them, small to medium-sized yolk-spheres are becoming enclosed in vacuolar-like spaces (Pl. I, fig. 4). One very interesting point about these processes, which is clearly brought out in Pl. III, figs. 16 and 17 of LC 3, is that they pass into direct continuity with the delicate cytoplasmic reticulum which pervades the marginal zone, and in which its yolk-spheres are situated.

Those vitellocytes which are in continuity in pairs take the form of elongated band-like structures, which may reach a length of up to 0.148 mm. and a maximum thickness of about 0.015 mm. Each band contains two nuclei, one situated towards its proximal end where it is thickest and one towards its thinner distal end. The thicker proximal portion of the band may be taken to represent the original or parent vitellocyte. Its cell-body, following on the division of the nucleus, has evidently grown outwards in the form of a thin process, carrying one of the daughter-nuclei with it, and so we reach the condition here seen, of a normal-sized vitellocyte situated adjacent to the disc-margin, in continuity with a much smaller vitellocyte lying peripherally to it, and to which it has given origin.

We conclude that the vitellocytes arise in the first instance by the division of marginal cells of the disc, and that they themselves are capable of increasing in number by division.

It may be noted that the isolated vitellocytes are sometimes limited on their outer and inner sides by distinct grooves, which are possibly to be regarded as transitory cleavage furrows.

LC 2 (J.15.8.30). (Pl. I, figs. 6-8; Pl. II, figs. 9-11, 12*a, b, c, d.*)

(Diameter of egg 4.2 mm. (fresh), 5.6 mm. (in alcohol). Diameter of blastodisc (from sections)  $0.46 \times 0.49$  mm. Thickness, 0.044 mm. (maximum). Shell, 0.006 mm. in thickness. Fixation, Bouin's Fluid.)

This disc, though differing from LC 1 in certain details, is in very much the same stage of development, and shows little or no advance on that. The lag in the division of the cytoplasm following on nuclear division is here even more accentuated, and adds greatly to the difficulty, not only of enumerating the blastomeres but of referring them to their categories, so that the following figures must be regarded as approximate only. The total number of actual or potential cells entering into the constitution of the blastodisc appears to be about 39. Of these, we estimate some 21 are superficial central disc-cells, 6 are potential deep, and 12 are marginal, compared with 27, 4, and 10 respectively in LC 1.

The central disc-cells have the same flattened oval form, and the same relations as in LC 1 (Pl. I, figs. 6, 7, 8). They mostly lie in contact, and their cytoplasm is yolk-free, though below, where the cells are in continuity with the yolk-bed, fine yolk-spheres in small numbers may be included in it. In this respect the peripheral disc-cell (*pd.*), on the right in Pl. I, fig. 6, is exceptional. Here the cleavage furrows seem to have extended more deeply into the yolk-bed than is usual, and so the lower and larger portion of the cell-body is crowded with small yolk-spheres, whilst its upper part, in which the nucleus is situated, is yolk-free.

All the central disc-cells with the exception of four are still in continuity with the yolk-bed, though some of them are in process of separation. The four cells excepted have become isolated, not only from the yolk-bed but also from their related sister-cells. One of the four ( $0.096 \times 0.021$  mm. in diameter, nucleus  $0.012 \times 0.006$  mm.) is seen in Pl. I, fig. 6, *c. 9*, directly overlying its hemispherical deep sister-cell, *c. 10* ( $0.057 \times$  about  $0.036$  mm. in diameter, nucleus  $0.012 \times 0.006$  mm.), the peripheral zone of which is laden with fine yolk-spheres, and which is in broad continuity with the yolk-bed. Two others appear in Pl. I, figs. 7 and 8. One of these (labelled *c. 1* in the figures, and measuring  $0.069 \times 0.024$  mm. in diameter, nucleus  $0.015 \times 0.006$  mm.), partially overlaps its deep sister-cell (*c. 11*) which lies obliquely below it, and measures  $0.051 \times 0.018$  mm. in diameter. The other of the two (*c. 2* in the figures) is larger than *c. 1* (measuring  $0.096 \times 0.024$  mm. in diameter, nucleus  $0.015 \times 0.006$  mm.), and likewise partially overlaps its sister-cell (*c. 3*), situated obliquely below it and open to the yolk. This cell we regard as deep, even though it reaches the surface two sections farther on in the series (Pl. II, figs. 9 and 10, *c. 3*). In this case the cleavage plane must have been obliquely vertical. The remaining cell of the four ( $0.10 \times 0.024$  mm. in diameter, nucleus  $0.012 \times 0.0045$  mm.) is situated at the margin of the disc (Pl. II, fig. 9, *c. 4*), and very slightly overlaps a small yolk-laden deep cell (*c. 5*) ( $0.051 \times 0.015$  mm. in diameter, nucleus  $0.009 \times 0.005$  mm.) which is widely open to the yolk.

It is evident that in these four cases the parent blastomere, whilst still open



to the yolk, has divided unequally in a plane more or less oblique to the surface, into a larger superficial cell and a smaller deep cell which still remains in continuity with the yolk-bed.

Of the 21 central disc-cells, 13 are uninucleate, 2 are still connected by a cytoplasmic bridge underlying a superficial groove, 1 is connected by a thin bridge underlying a deep, curved tangential groove with its parent marginal, and 2 are connected with each other as well as with the parent marginal. This latter (with a long diameter of 0.056 mm.) is bounded by a deep cleavage groove on its outer side; it stains rather deeply, contains sparse yolk-granules in its superficial cytoplasm, and is in broad continuity with the yolk-bed. On its inner side it becomes continuous by a narrow neck, situated below a deep groove, with a small disc-cell (long diameter 0.048 mm.), and this is continuous with a still smaller cell (long diameter 0.032 mm.), a shallow furrow separating the two. Both these small cells are widely open to the yolk-bed, and both fail to reach the surface. Possibly they should be regarded as prospective deep cells. This seems to be a case of the division of a marginal cell into a daughter-marginal and a central disc-cell, the latter having subsequently divided unequally into two.

Two other superficial cells (Pl. I, fig. 6, *c.* 6 and *c.* 7) exhibit curiously complicated relations, resulting from delay in cytoplasmic division. The two cells in question are still in continuity with each other by a thick bridge, underlying a fairly deep, wide groove, and both are in continuity below with an elongated, roughly dumb-bell-shaped mass of cytoplasm about 0.12 mm. in length, and containing two nuclei, one in each bulbous end, so that each superficial cell more or less overlies a potential deep cell, and all four are in cytoplasmic continuity. The left superficial cell (Pl. I, fig. 6, *c.* 6) is no longer directly connected with the yolk-bed, and is marked off by a circular groove from the deep cell with which it is in continuity, and which lies slightly obliquely below it, the plane of separation being nearly horizontal. The right superficial cell *c.* 7 is still in continuity with the yolk-bed and only partially overlies its related deep cell, which is disposed very obliquely below it, so that in Pl. I, figs. 7 & 8 and Pl. II, fig. 9 (*c.* 8) it appears isolated.

The remaining cell of this category is large ( $0.084 \times 0.028$  mm. in diameter), is connected with the yolk-bed only over its central region, and overlies very obliquely a deep cell ( $0.054 \times 0.030$  mm. in diameter), from which it is marked off by a faint line of separation.

The central cells are on the average a little larger than those of LC 1, the average diameter of 12 cells measured being  $0.070 \times 0.027$  mm., and that of the nucleus  $0.012 \times 0.0056$  mm.

Of the six potential deep cells present in the disc, five have been referred to above. Two of these (Pl. I, fig. 6, *c.* 10 and Pl. II, fig. 9, *c.* 5) are of interest in that they are rich in fine yolk-spheres, are more or less hemispherical in form, and appear more intimately connected with the yolk-bed than the others. It is possible that the sub-disc cells which appear in LC 4 originate by the division of deep cells of this type. One of the five was described as reaching the surface (Pl. II, fig. 10, *c.* 3), and a second example of the same condition is provided by the last member of the series. This deep cell is large ( $0.072 \times 0.021$  mm. in diameter, nucleus  $0.009 \times 0.004$  mm.), and obliquely underlies about three-quarters of its

superficial sister-cell, which is still larger ( $0.108 \times 0.024$  mm. in diameter, nucleus  $0.012 \times 0.0045$  mm.), and is almost completely isolated from the yolk-bed. The deep cell is largely marked off from it by a slightly oblique line of separation and a peripheral groove, and reaches the surface at one of its ends.

*Marginal cells.*—In our enumeration of the disc-cells we have listed some 12 as marginals, but that number is probably excessive, since it is difficult to distinguish between parent marginals and their peripherally situated derivatives. Two are in process of division by radial furrows to form peripheral disc-cells (Pl. II, fig. 11), and at the same time the cell on the right in the figure is connected by a thin cytoplasmic stalk (about 0.05 mm. in length) with a vitellocyte ( $0.054 \times 0.024$  mm. in diameter, nucleus  $0.013 \times 0.006$  mm.), to which it has given origin. Three are in process of tangential division, one (referred to below) to form a marginal or peripheral cell and a vitellocyte, and two to form each a peripheral and a central cell.

*Vitellocytes.*—These number about 21, of which 11 are isolated (Pl. II, figs. 9 & 10, *pv.*), 2 are paired (in process of division and incompletely separated), 4 are binucleate, and 2 are still connected with their parent marginals.

Figs. 12 *a*, 12 *b*, 12 *c*, and 12 *d* (Pl. II) form a series illustrating the condition, already described in LC 1, where a vitellocyte in process of division has assumed an elongated band-like form. Pl. II, fig. 12 *a* shows what we take to be a peripheral disc-cell (*pd.*) ( $0.072 \times 0.033$  mm. in diameter, nucleus  $0.010 \times 0.008$  mm.), on the right of the figure, separated on its outer side by a deep cleavage furrow from a large vitellocyte (*pv.*) ( $0.060 \times 0.025$  mm. in diameter, nucleus  $0.012 \times 0.004$  mm.). Presumably these two cells are sister-cells, formed from a parent marginal by tangential division. The cytoplasmic process given off from the left side of the vitellocyte can be followed through figs. 12 *b* and 12 *c* (Pl. II,) until it terminates in the daughter-vitellocyte (*pv.* 1) ( $0.054 \times 0.018$  mm. in diameter, nucleus  $0.012 \times 0.004$  mm.), seen in Pl. II, fig. 12 *d*, the total length of the two being about 0.11 mm. In another example of the same condition, the combined length of the two is 0.10 mm. In yet another case, a large marginal cell ( $0.088 \times 0.03$  mm.) is connected by a narrow band of cytoplasm underlying a wide tangential fissure with an elongated cell ( $0.090 \times 0.021$  mm. in diameter, nucleus  $0.010 \times 0.0035$  mm.), with sparse fine yolk-spheres in its superficial cytoplasm, and a few larger spheres in its deep cytoplasm. This cell we regard as a potential vitellocyte in process of separation from its parent marginal.

LC 3 (VVH 21). (Pl. II, figs. 13, 14, 15; Pl. III, figs. 16 & 17.)

(Diameter of egg, 4.5 mm. (fresh),  $5.60 \times 5.25$  mm. (in alcohol). Diameter of blastodisc (from sections),  $0.45 \times 0.44$  mm. Thickness,  $0.047 \times 0.060$  mm. Shell, about 0.006 mm. in thickness. Fixation, Bouin-Hollande.)

The entire egg was sectioned; the serial sections of the disc are good and the cytological fixation is excellent, but the fixative employed has the disadvantage that it fails to harden the yolk-mass, causing it to swell and disintegrate.

This disc is definitely in advance of the two preceding discs in the following respects: (1) the number of cells forming the disc has increased to 48; (2) out of 18 superficial central cells, 8 are now completely delimited; (3) the deep cells have increased to 14, of which 6 are delimited from their related superficial cells;



(4) it is no longer possible to distinguish marginal cells as originally defined; (5) the deep cells as well as many of the superficial cells contain considerable amounts of fine yolk-spheres, similar to and evidently derived from those present in the yolk-bed.

Pl. II, fig. 13 provides a surface view of the disc, based on photographs and study of the specimen under the stereoscopic binocular microscope. It shows that the disc consists of a central group of smaller blastomeres (superficial central) surrounded by a quite irregular, discontinuous ring of larger elements, varying greatly in size (peripheral disc cells). Outside this ring and separated from it by a space (really a groove) of varying width, and best marked on the lower side of the figure, a second ring is indicated by the presence of a series of lightish areas, ovalish or rounded, and isolated from each other. These evidently mark the sites of the larger of the vitellocytes, which are present to the number of about 24 around the periphery of the disc.

An enumeration of the cells in the serial sections shows that the disc consists approximately of 48 cells, of which we regard 18 as superficial central cells, 16 as peripheral disc-cells, and 14 as deep cells. Curiously enough, the average diameter of 12 superficial cells measured is precisely the same as in LC 2, viz.:  $0.070 \times 0.027$  mm., but their nuclei are larger, averaging  $0.015 \times 0.008$  mm.; the cells range in diameter from  $0.060 \times 0.025$  mm., nucleus  $0.015 \times 0.006$  mm. to  $0.090 \times 0.030$  mm., nucleus  $0.018 \times 0.010$  mm.

The central cells are mostly oval or oblong in outline, are well marked off from each other, and form a fairly continuous superficial layer, with only occasional gaps (Pl. II, figs. 14 & 15). Eight out of the 18 cells are delimited from the deep cells as well as from the yolk-bed, and others are in process of becoming so. In many of them a localized vacuolated area, rich in fine yolk-spheres, is present in the lower half of the cell-body.

The peripherally situated cells to the number of 16, which form the above-mentioned discontinuous ring enclosing the group of central cells, occupy the site of the marginal cells of the preceding stages (Pl. II, figs. 14 & 15, *pd.c.*). Eight of them, characterized by their rich yolk-content and large size (their range in diameter being from  $0.069 \times 0.024$  mm., nucleus  $0.015 \times 0.012$  mm. to  $0.11 \times 0.042$  mm., nucleus  $0.018 \times 0.009$  mm.), we originally regarded as marginals (Flynn & Hill, 1941, p. 235), but since all of them except one are bounded on their outer sides by more or less wide peripheral grooves (Pl. II, figs. 14 & 15, *gr.*), and some of them show indications of becoming delimited below, they no longer strictly conform to the original type, and it seems better to group them with the other peripherally situated cells as peripheral disc-cells. One of them is binucleate.

The deep cells (Pl. II, figs. 14 & 15, *dpc.*) have increased from 6 in LC 2 to 14, and of these, 6 have become separated from their related superficial cells which they obliquely underlie, whilst others are in process of becoming delimited. All the deep cells except one are still in continuity with the yolk-bed, but in some of them the cell-membrane is beginning to extend round so as to mark off the cell-body from the underlying fine yolk. One deep cell is in very oblique continuity with a peripheral disc-cell, and another, situated at the periphery of the disc, gives off an outwardly directed process ( $0.066$  mm. in length), possibly destined to form a vitellocyte. The deep cells, like the superficial, only in much more

marked degree, show localized areas of vacuolation in their cytoplasm, rich in fine yolk-spheres identical with those in the yolk-bed. The latter structure clearly plays an important part in providing the rapidly growing blastomeres with the nutrient material they require.

Pl. II, fig. 14 illustrates a section passing just to one side of the centre of the blastodisc. The latter is seen to be bounded on each side by a well-marked peripheral groove (*gr.*). Centrally a gap occurs in the superficial layer, floored by a deep cell. Six superficial cells (four central and two peripheral) and four deep cells are present in the figure. The peripheral cells (*pd.*) are large, contain much yolk (mostly fine) in their lower halves, and sparse fine spheres in their superficial cytoplasm, and are in continuity with the yolk of the marginal zone below, though they show indications of becoming delimited. The right peripheral cell (*pd.*) is in continuity at its lower left corner with a deep cell which lies very obliquely below and to the left of it. Three of the deep cells are isolated from their related superficial cells, and the fourth (second from the left) is all but completely separated. They are all in continuity with the yolk-bed, though limiting cell-membranes are beginning to appear on the lower surfaces of the cells on the right. They are more or less richly vacuolated, and contain numerous minute yolk-spheres, often forming localized groups. Just outside the limiting groove on each side a vitellocyte (*pv.*) is visible.

Pl. II, fig. 15 depicts the seventh section to one side of that shown in the preceding figure, and exhibits very similar features. Seven superficial cells are visible (five central and two peripheral), together with three deep cells. The large ovoidal superficial cell (*c. 1*) on the left contains an aggregation of fine yolk-spheres on one side of its deep half, and is becoming delimited from the yolk-bed. The oblong superficial cell (*c. 2*) next to it obliquely overlies a deep cell from which it has largely become separated. Adjoining the latter and situated at a slightly lower level is a second deep cell (*dpc.*), which is free from and very slightly overlapped by a superficial cell, the periphery of which is just visible in the figure. To the right of the latter is an oval superficial cell (*c. 3*), delimited from the yolk-bed, and adjoining it on the right is another superficial cell (*c. 4*) which is in continuity with the underlying deep. Lastly, in contact with the peripheral cell (*pd.*) on the right is a superficial cell (*c. 5*), much vacuolated below, and containing fine dispersed yolk-spheres, which is in continuity with the yolk-bed. On the left a single vitellocyte (*pv.*) is present.

*Vitellocytes.*—The vitellocytes (Pl. II, figs. 14 & 15; Pl. III, figs. 16 & 17, *pv.*) now number about 24 and are well developed. They vary considerably in size, ranging from small cells  $0.012 \times 0.006$  mm. in diameter, nucleus  $0.008 \times 0.006$  mm., to quite large cells, up to  $0.069 \times 0.021$  mm. in diameter, nucleus  $0.018 \times 0.009$  mm. They lie adjacent to the disc-margin, just outside the groove (*gr.*) limiting the peripheral cells, and close below the zona-albumen layer (Pl. II, fig. 14), though a few are more deeply situated.

Structurally they differ in no essential respect from those of LC 1 (*ante*, p. 11). From Pl. III, figs. 16 & 17 it will be seen that the cytoplasm exhibits the same uniformly staining, finely granular character as in them, but below the upper surface of the cell vacuolation tends to be somewhat more marked, and the yolk-spheres there situated are rather less numerous and more varied in size.



The nucleus, oval or elliptical in form, is large, stains deeply, and is rich in coarse, rounded nucleolar granules, strongly basophil. The cytoplasmic processes which arise from the periphery and under-surface of the cell-body exhibit the typical relations. Delicate and tapering, they extend out between the yolk-spheres adjoining the cell-body, and anastomose with each other so as to enclose the spheres in vacuolar-like spaces. In this egg they can readily be traced into continuity with the delicate cytoplasmic reticulum containing fine yolk-spheres, which extends throughout the yolk-bed, including the marginal zone, and which is here remarkably well preserved (Pl. III, fig. 17, *cre.*).

On one side of the disc a few vitellocytes occur clumped together, and are so connected by their processes that they present the appearance of a syncytial network. One vitellocyte is so exceptionally large ( $0.120 \times 0.027$  mm. in diameter, nucleus  $0.015 \times 0.009$  mm.) as to suggest its origin by direct transformation from a marginal cell.

LC 4 (B.1.8.30). (Pl. III, figs. 18–20.)

(Diameter of egg, 4.5 mm. (fresh), 5 mm. (in alcohol). Diameter of disc,  $0.49 \times 0.54$  mm. Thickness, 0.049 mm. Shell, 0.006 mm. in thickness. Fixation, Bouin's Fluid.)

The enumeration of the cells in the blastodisc has proved difficult owing to certain defects in the series, and the numbers arrived at must be regarded as very approximate, an under- rather than an over-estimate.

This disc exhibits an advance on LC 3 in the following features: (*a*) the disc-cells number about 56 as compared with 48 in the latter, (*b*) eight of the 12 deep-cells present are delimited from the yolk-bed, (*c*) the number of vitellocytes situated peripherally to the disc has increased to 32 as compared with 24 in LC 3, but in addition 7 vitellocytes are now present below the periphery of the disc (sub-marginal vitellocytes), (*d*) free cells to the number of about 14 have made their appearance in the yolk-bed, immediately below the disc, 10 out of the 14 underlying its more central region. These free cells we propose to term "sub-disc cells."

Pl. III, figs. 18 & 19 illustrate the sectional appearance of the disc; the former shows the central region of a section passing approximately through its centre, and the latter, four sections to one side of the centre, includes the periphery of the disc (on the left side in the figure). Pl. III, fig. 20 shows the peripheral region of the disc on the opposite (right) side, in a section still more remote from the centre.

The disc is thickest centrally, where it is in places two cells thick, whilst peripherally it is never more than one cell thick. The blastomeres number about 56, of which 44 are superficial, 10 more than in LC 3, and about 12 are deep.

The superficial disc-cells are for the most part oval or oblong in outline, and only very occasionally flattened. There are a few gaps in the disc where the cells fail to meet, but otherwise they lie in apposition, and are mostly well marked off from each other. The great majority of them are clearly delimited from the yolk-bed, about eight cells only being still open to the latter. A few of the superficial cells are still in continuity with their deep sister-cells (Pl. III, fig. 18, *dpc.*). Their cytoplasm is more or less vacuolated, especially peripherally, and may contain very fine yolk-granules in variable quantity.



The average diameter of 20 disc-cells is  $0.045 \times 0.020$  mm., and that of the nucleus  $0.010 \times 0.007$  mm., measurements strikingly smaller than those recorded for the disc-cells in LC 3. The peripheral disc-cells tend to be large and rich in fine yolk-spheres (Pl. III, fig. 20, *pd.*). They are usually marked off from the yolk of the marginal zone by a more or less distinct peripheral groove, and some of them are delimited below.

Close to the periphery of the disc on one side is a rather deeply situated cell which fails to reach the zona-albumen layer, being separated therefrom by a space occupied by coagulum. It is hemispherical in section and large ( $0.060 \times$  about  $0.024$  mm. in diameter, nucleus  $0.013 \times 0.009$  mm.), and is broadly continuous with the yolk-bed. Its cytoplasm is vacuolated and rich in fine yolk-granules, except round the nucleus. We mention this cell because it is comparable with the similar cells noted in LC 2, and like them seems to be a belated blastomere of early cleavage stages which has failed to become delimited or to divide.

*Deep cells.*—These, as noted above, number about 12. They lie either directly or obliquely below their superficial sister-cells. Eight of them are isolated from the yolk-bed, whilst four are still in continuity with the same, and also with their superficial sister-cells. In Pl. III, fig. 19 the deep cell (*dpc.*) with a darkly stained nucleus, which obliquely underlies and is continuous with its superficial sister-cell, seems to be in process of becoming delimited from the yolk-bed. One isolated cell is binucleate. Like the superficial, the deep cells are vacuolated, sometimes markedly so (Pl. III, fig. 18, *dpc.*), and contain more or less numerous fine yolk-granules.

*Vitellocytes.*—There are now about 32 vitellocytes situated peripherally to the disc, an increase of 8 in this position as compared with LC 3, and in addition there are present some 7 vitellocytes which have migrated inwards below the periphery of the disc instead of outwards below the egg-membrane. These sub-marginal vitellocytes differ in no way structurally from the peripheral, and are confined to a zone below the periphery of the disc, not exceeding 0.10 mm. in width.

The vitellocytes in this egg are not so well developed as in LC 3, and are mostly small, with scanty cytoplasm and rather shrunken nuclei in which the chromatin granules are adherent to the nuclear membrane, so causing it to appear thickened. The peripheral vitellocytes lie at variable distances from the margin of the disc (in one instance as far out as 0.28 mm. from the same), and are mostly situated close below the egg-membrane, though a few are more deeply situated in the yolk. Two of the sub-marginal vitellocytes are binucleate.

*Sub-disc cells.*—In addition to the sub-marginal vitellocytes, we encounter in this stage, for the first time, a number of cells ( $\pm 14$ ) which like them are situated in the yolk-bed, mostly close below the disc, though a few have migrated a little more deeply into the same, *e. g.*, the cell on the right in Pl. III, fig. 19 (*sdc.* 1) lies 0.048 mm. below the surface of the disc, whilst the deepest cell in Pl. III, fig. 18 (*sdc.* 3) is 0.054 mm. below the surface and 0.022 mm. below the lower limit of the disc. They occur mainly below the central region of the latter, 4 only out of the 14 occupying positions varying from 0.09 to 0.013 mm. within the disc-margin. Though, in this stage it is not possible to draw any very sharp line of distinction between these cells and the sub-marginal vitellocytes, they differ from

the latter in certain points of detail and in the next stage, LC 5 are clearly distinguishable from them. We therefore propose to speak of them as "sub-disc cells." Their cell-body is, on the whole, rather richer in cytoplasm than that of the sub-marginal vitellocytes, and is formed of a perinuclear zone of yolk-free cytoplasm, varying in width in different cells, outside which there is sometimes recognizable a more or less distinctly organized zone, rich in fine yolk-granules (Pl. III, fig. 18, *sdc. 3*, *sdc. 5*; fig. 19, *sdc. 2*). Their nuclei, like the cells themselves, vary considerably in diameter (from about  $0.006$  to  $0.011 \times 0.008$  mm.), and are mostly plump, with a smooth, non-wrinkled nuclear membrane, and stain rather deeply. The sub-disc cell on the right in Pl. III, fig. 19 (*sdc. 1*) has a diameter of about  $0.018$  mm., and possesses two overlapping nuclei (with diameters of  $0.011 \times 0.008$  and  $0.009 \times 0.007$  mm. respectively). In another binucleate cell the nuclei measured  $0.012 \times 0.007$  and  $0.011 \times 0.006$  mm. in diameter.

The chief interest of these cells centres in the question of their origin, and whether or not those of them that remain close below the disc eventually become included in the same as deep cells. In Pl. III, fig. 18 three such cells are seen lying in the vacuolated central portion of the yolk-bed. The deepest of the three (*sdc. 3*) has been referred to above. It lies  $0.054$  mm. below the upper surface of the disc, and has a diameter of about  $0.012$  mm., that of its nucleus being  $0.0075$  mm. Above it and slightly to the left (in the figure) is a small cell (*sdc. 4*), with a deeply stained round nucleus (with a diameter of  $0.006$  mm.), and scanty cytoplasm around it. It lies close below the lower limit of the disc, directly below the greatly vacuolated deep cell labelled *dpc.* in the figure. The third cell (*sdc. 5*) lies slightly above and to the right of cell *sdc. 4*. Its nucleus ( $0.011 \times 0.005$  mm. in diameter) is oblong, appears slightly constricted in its middle, and is enclosed in a thin layer of cytoplasm. The immediately surrounding zone of the yolk-bed (vacuolated and containing fine yolk-granules) forms on its upper side a definite convex projection directly underlying a large superficial cell. If this sub-disc cell with its surrounding area were to become delimited below, a deep cell would be added to the disc. Very similar relations are seen in the cell underlying a gap in the superficial layer in the right half of Pl. III, fig. 19 (*sdc. 2*), which also seems to belong to the sub-disc category. It consists of a small central mass of yolk-free cytoplasm enclosing the nucleus ( $0.010 \times 0.008$  mm. in diameter), and here again, the surrounding zone of the yolk-bed forms on its upper side a convex bulging directed towards the above-mentioned gap.

This stage provides no conclusive evidence as to the origin of these sub-disc cells. The possibility that they and the sub-marginal vitellocytes alike are simply vitellocytes, derived from the original marginal cells of the early blastodiscs which have wandered inwards below the disc, instead of outwards below the egg-membrane, is largely discounted by the fact that in LC 5 the sub-disc-cells differ widely in their appearance and structure from the sub-marginal vitellocytes. A more probable explanation is that they arise *in situ*, so to speak, as the result of the division of disc-cells or deep disc-cells, prior to their separation from the yolk-bed, the uppermost of the two daughter-cells rounding off and becoming included in the disc, whilst the lowermost remains open to the yolk-bed and sinking down, or even migrating deeper into it, forms directly a sub-disc-cell, or again it may itself subsequently divide to form a deep disc-cell and an underlying



sub-disc. In favour of this mode of origin it may be noted (1) that 10 out of the 14 cells we have referred to this category are situated below the more central, thicker region of the disc, (2) that the great majority of them lie close below its lower limit, (3) that they tend to have a positional relationship to the overlying disc-cells, *i. e.*, they tend to lie directly or only slightly obliquely below them, and (4) that there are present in LC 2 and in this stage deeply situated disc-cells which are in broad continuity with the yolk-bed, each of which on division could give origin to an upper disc-cell and a lower sub-disc.

We think it probable that some few of the sub-disc cells which remain close below the disc eventually become delimited from the yolk and included in the disc. We shall find, however, when we come to the next stage, LC 5, that, whilst some of them remain superficially situated in the yolk-bed, others have migrated fairly deeply into the same, and we shall further find in much later stages, including those belonging to Group V, that cells and nuclei in a more or less degenerate condition occur sporadically, and in very varying numbers in the superficial region of the yolk-bed, less frequently in its deep region. But to what extent (if any) they are derived from the sub-disc cells under consideration, and to what extent from inwandered sub-marginal vitellocytes, is difficult to determine, though the close relationship that many of them exhibit to the yolk-membrane suggests that they are in the main of vitellocyte origin. Because of the possibility of their mixed origin, we shall refer to the cells which occur in the yolk-bed in later stages as "yolk-bed cells," or where their cytoplasmic bodies are not distinctly recognizable, as "yolk-bed nuclei."

As concerns the significance of the sub-disc cells, they would seem to correspond to the free cells variously known as merocytes, merocyte nuclei (Virchow (1892), Peter (1938)), yolk nuclei (Will (1895)), etc., which are of general occurrence in the yolk underlying the sub-germinal cavity and the early blastoderm in the Reptilian egg. The observations of Virchow (1892) and Will (1895) have shown that in *Lacerta* they are destined to give origin to the post-cleavage (*Nachfurchung*) cells which are budded off from the surface of the yolk into the sub-germinal cavity, to become incorporated in greater part in the endoderm, the remainder undergoing degeneration.

Will (*loc. cit.*, p. 22) expresses the view that these yolk-cells (*Dotterkerne*) are derived from the cleavage cells, though of this he has no positive evidence to offer.

LC 5 (A.15.7 30.) (Pl. III, fig. 21 ; Pl. IV, figs. 22-24.)

(Diameter of egg, 4.9 mm. (fresh), 5.5 mm. (in alcohol). Diameter of disc,  $0.41 \times 0.40$  mm. Thickness, 0.064 mm. Shell, 0.008 mm. in thickness. Fixation, Bouin's Fluid.)

This disc, in its surface dimensions, is the smallest of those included in the Group. The serial sections are not quite perfect, so that it has not been possible to make an accurate count of the disc-cells.

Developmentally the disc is separated by a considerable gap from the preceding stage, as is indicated by its increase in thickness, and also by the increase in the thickness of the shell. In the interval the disc has been the seat of a remarkable burst of mitotic activity, as the outcome of which it has attained a thickness of from four to five cells in its central region, as compared with a thickness of two

in LC 4, the main increase having taken place in the deep disc-cells. A further outcome of this activity is that the disc-cells are now smaller than in LC 4, the average diameter of 15 cells being  $0.030 \times 0.013$  mm., and that of their nuclei  $0.0098 \times 0.0052$  mm.

Pl. III, fig. 21 illustrates a section passing approximately through the centre of the disc and including the periphery on the right side; Pl. IV, fig. 22 illustrates the third section to one side of Pl. III, fig. 21, and includes both margins of the disc. From these figures it will be seen that the disc attains its maximum thickness (0.064 mm.) over a limited area in its central region, where it takes the form of a downwardly projecting irregular knob-like thickening, composed of from four to five superimposed cells.

Peripherally to this central region, the disc thins out in an irregular fashion to a thickness of about two cells, and eventually to a single cell at the margin. As in LC 3 and 4, true marginal cells are no longer distinguishable.

It will further be seen from the figures that the under-surface of the disc is extremely irregular, and lacks a definite contour-line, except over the central region in Pl. III, fig. 21 directly overlying the vacuolated core of the yolk-bed. Here, over a very restricted area about 0.20 mm. in width, and extending through only a few sections, the under-surface of the central region is fairly smooth and even, and the deep cells are clearly marked off from the yolk-bed by a definite line of demarcation. The appearance of this line heralds the commencing delimitation of the disc from the yolk-bed, and is due to the differentiation on the surface of the latter of an extremely delicate pellicle, or membrane (the yolk-membrane as we may term it), between which and the deep cells very narrow clefts are occasionally present. Its formation is no doubt induced by the rounding off and separation of the deep cells from the yolk-bed. It appears to be of the same nature as the egg-membrane (*vide* Part IV, p. 463) which encloses the yolk, and in some sections where the yolk-membrane is already distinguishable below the periphery of the disc it can be seen to pass into direct continuity with it (Pl. III, fig. 21, right side of figure).

Outside the delimited central area the irregular uneven character of the under-side of the disc results largely from variations in its thickness, and the consequent varying extent to which the deep cells project down into the yolk-bed (*cf.* Pl. IV, figs. 22, 24). At first sight it looks as if prolongations of the latter were actively penetrating amongst the cells, but this is an appearance only, though possibly some infiltration of yolk-spheres between them does actually occur.

In the central region of the disc the superficial cells vary in size, and are mostly flattened and quadrangular or oblong in outline, with correspondingly flattened nuclei. They lie in close contact so as to form a continuous superficial layer which peripherally becomes somewhat thicker, the cells assuming a more oval form. In some of the cells fine peripherally situated yolk-granules are present.

Immediately below the superficial layer, in the central region, the deep cells still tend to be flattened in places and compactly arranged (Pl. IV, fig. 22), but deeper down they become larger, more oval or rounded in outline, and are irregularly arranged, about two deep. They are often vacuolated peripherally, and some of them contain fine yolk-granules. Their nuclei are oval or rounded in form, and not flattened like those of the more superficially situated cells. Though



many of the deep cells adjoining the yolk-bed are more or less clearly delimited, others are still in continuity with the same.

We have observed three deep disc-cells in mitosis. One is seen in Pl. IV, fig. 22. It is not sharply limited from the yolk-bed and is in the metaphase with the equatorial plate so disposed that the plane of division would be horizontal, with resulting formation of two superimposed deep cells. A second is seen in Pl. IV, fig. 23, the indicated plane of division being vertical to the surface. In the superficial layer, only one cell has been encountered in division, a peripheral cell in the telophase.

At the periphery of the disc the peripheral disc-cells may contain only sparse, fine yolk-granules or none (Pl. III, fig. 21, Pl. IV, fig. 22, *pd.c.*), or on the other hand, they may attain a considerable size (up to  $0.045 \times 0.027$  mm. in diameter, nucleus  $0.010 \times 0.006$  mm.), and contain numerous yolk-spheres. The majority of the cells of this type are crowded with moderately large spheres intermingled with fine, and appear poor in cytoplasm, whilst a few are much richer in cytoplasm and contain numerous fine peripherally situated yolk-spheres. They lie either actually at the periphery of the disc in contact with the zona-albumen layer, when they are mostly well delimited, or they are situated more deeply (Pl. IV, fig. 22 (*c*)), and may even be sub-marginal. Most of them are not sharply marked off from the yolk-bed.

These yolk-rich cells, of which some 17 or more are present in this disc, are no doubt derivatives of the marginal cells like the vitellocytes. Indeed, some of the cells, especially those with coarse and fine yolk, might easily be mistaken for the latter but for the fact that they are provided with limiting membranes. Here and there, the yolk-membrane is quite distinct below the periphery of the disc, though it extends inwards for only a very short distance (Pl. III, fig. 21, right side of figure).

*Sub-disc cells.*—There are from 10 to 12 cells in this disc which appear referable to this category, of which six lie more or less deeply in the yolk-bed, and the remainder close below the disc. The former (deep sub-disc cells) offer no difficulties of interpretation, but it is otherwise with the latter, since it is difficult in some cases to decide whether a particular cell should be regarded as a sub-disc or simply as a deep disc not yet delimited from the yolk-bed, but if the sub-disc cells originate from disc-cells in the way we have suggested above (*ante*, p. 19), no sharp line of distinction between the lowermost of the deep cells and the sub-disc cells located close below the disc is to be expected.

In this egg the sub-disc cells are larger and much better developed than in the preceding stage, and are easily distinguishable from the vitellocytes, to which, indeed, they appear to be in no way related.

A rather exceptional cell which may be a sub-disc or a deep disc not yet completely delimited, and which recalls the deep-seated disc-cells to which we have called attention in LC 2 and 4, is seen in Pl. IV, fig. 24 (*dc.*). It takes the form of a large, somewhat flattened, convexly projecting cell ( $0.060 \times$  about  $0.024$  mm. in diameter), with a large, oval nucleus ( $0.012 \times 0.008$  mm. in diameter), which is richly laden with yolk-spheres, and is in continuity with the yolk-bed, except possibly towards one end (left), where it seems to be becoming delimited. In the figure it will be seen that this cell lies in contact with, and on the same level as a

clear vacuolated cell (*dpc.*) ( $0.042 \times 0.028$  mm. in diameter, nucleus  $0.009 \times 0.007$  mm.), which is continuous above with its obliquely overlying sister-cell, and is clearly to be regarded as a deep disc.

Two cells which we have referred with rather more confidence to the sub-disc category, and which may be taken as typical of the others, are seen in Pl. IV, fig. 23. One of them (*sdc.* 1) lies close to the right margin of the disc, in contact with two overlying deep disc-cells. It measures approximately  $0.039 \times 0.024$  mm. in diameter, nucleus  $0.008 \times 0.006$  mm. The nucleus which is not flattened but plump and irregularly ellipsoidal, lies in the central yolk-free area of the cell-body, outside which the peripheral region of the cell is crowded with fine yolk-spheres, intermingled with coarser spheres on the lower side, where it is in open continuity with the yolk-bed. The second cell (*sdc.* 2) ( $0.042 \times$  about  $0.027$  mm. in diameter, nucleus, spherical,  $0.009 \times 0.008$  mm.) lies towards the left in the figure directly below a deep disc-cell in the metaphase, and resembles the first in all essentials, except that its prospective limits are less clearly indicated. It seems likely that both these cells will eventually become included in the disc.

Another deep-seated cell deserving of brief mention is seen in Pl. IV, fig. 22, underlying the marginal region of the disc, on the left side (*sdc.* 3). This cell lies isolated in the yolk-bed, below the apparent lower limit of the disc, and is not sharply delimited. Its cytoplasmic body is large ( $0.027 \times 0.024$  mm. in diameter, nucleus  $0.009 \times 0.006$  mm.) and vacuolated peripherally, where it contains sparse yolk-granules. Though from its position possibly destined to be incorporated in the disc, this cell has the characters of a deep sub-disc, and closely resembles the cell of this type seen in the lower left corner of Pl. III, fig. 21 (*sdc.* 5), except that the latter is trinucleate.

The six deep sub-disc cells which are present in this stage all lie isolated in the yolk-bed, well below the lower limit of the disc, a fact which shows that they have some power of migration. They vary in diameter from  $0.021$  mm. to  $0.036 \times 0.021$  mm., the latter measurement being that of the cell situated in the lower left corner of Pl. III, fig. 21 (*sdc.* 5). This particular cell lies  $0.14$  mm. below the surface of the disc, and is the most deeply situated of the six. It is trinucleate, possessing one larger oval nucleus  $0.009 \times 0.006$  mm. in diameter, and two smaller rounded nuclei. All the others are uninucleate; the nucleus tends to be large, attaining a diameter of up to  $0.12 \times 0.011$  mm. The cell-body (Pl. III, fig. 21 (*sdc.* 5), Pl. IV, figs. 22 (*sdc.* 4) & 23 (*sdc.* 6)) is relatively rich in cytoplasm, and in most of the cells presents a stellate appearance, owing to the presence of peripheral vacuoles separated by thin radiating strands of cytoplasm, which seem to pass into continuity with the cytoplasmic reticulum of the yolk-bed. Fine yolk-granules are also present in the peripheral cytoplasm.

The two deep sub-disc cells seen in Pl. III, fig. 21 (*sdc.* 5) and Pl. IV, fig. 22 (*sdc.* 4) are situated in the periphery of the central vacuolated core of the yolk-bed, whilst another lies deeply in the core itself. The cell seen in Pl. IV, fig. 22 (*sdc.* 4) shows well the stellate appearance of the cell-body. It lies  $0.093$  mm. below the surface of the disc, and has a diameter of about  $0.027$  mm., that of the nucleus being  $0.012 \times 0.009$  mm.

*Vitellocytes.*—We have recorded the presence of some 36 vitellocytes in this egg, of which 31 are peripheral and 5 sub-marginal, but an accurate count was not



possible owing to some slight damage to the peripheral region of the disc. They essentially resemble those of the preceding stage, being small, with scanty cytoplasm and rather shrunken nuclei. One of them is binucleate.

LC 6 (K.15.8.30). (Pl. IV, figs. 25 & 26 ; Pl. V, figs. 27 & 28.)

(Diameter of egg, 4.4 mm. (fresh), 5.1 mm. (in alcohol). Diameter of disc,  $0.48 \times 0.52$  mm. Thickness, 0.084 mm. Shell, 0.008 mm. in thickness. Fixation, Bouin's Fluid.)

This is an excellent disc, the serial sections are good and adequately stained. It is of greater surface-extent, and definitely thicker than LC 5. The increase in thickness is not due to an increase in the number of superimposed cells, the disc in both being about four cells thick, but to the larger size of the cells ; the average diameter of 15 disc-cells being  $0.040 \times 0.023$  mm., and that of their nuclei  $0.010 \times 0.007$ , as compared with the average diameter of the same number of cells in LC 5 of  $0.030 \times 0.013$  mm., nucleus  $0.0097 \times 0.0076$  mm. The greater diameter of this disc over LC 5 is of no developmental significance, since the size of the disc is subject to individual variation. Moreover, the disc of LC 5 is on the small side and below the average in diameter.

Perhaps the most striking features in this disc as compared with LC 5 are (1) the richness of the disc-cells in included yolk-spheres, which no doubt accounts for their increased size, and (2) the marked change in the character of the vitellocytes.

So far as the delimitation of the disc from the yolk-bed is concerned, this disc has made some slight but quite definite progress on LC 5. Its under-surface is now much less ragged and irregular, so that its lower limits are more readily determinable. Moreover, it has made much more definite progress than has LC 5 towards the attainment of a biconvex form, whilst the concavity in the yolk-bed in which it lies is now much more obvious than it was in that stage (Pl. IV, fig. 25).

As in LC 5, the disc is distinguishable into a thicker central region, about 0.25 mm. in diameter, and about four cells in thickness, which overlies the clear vacuolated central portion of the yolk-bed, and a much narrower and thinner peripheral region, three or four cells in width, and never more than two cells in depth (Pl. IV, figs. 25 & 26).

The disc-cells are larger, plumper, and less flattened than in LC 5. The superficial layer is composed of oval cells, lying for the most part in close contact, except in the peripheral region where gaps, sometimes of large size, may occur between them (Pl. V, fig. 27). In the central region the deep cells are fairly compactly arranged, but in the peripheral region large spaces are present between them in many of the sections, not all of them artefacts (Pl. IV, fig. 25 and Pl. V, fig. 27).

Many of the cells, especially the deep central, are more or less vacuolated, and are rich in peripherally situated yolk-spheres, mostly fine in the central cells, coarser and more numerous in the peripherally situated cells (Pl. V, fig. 27). The marked increase in the yolk-content of the disc-cells is one of the most striking features of this stage, and the question arises, how has it come about ? The inclusion of yolk-spheres in deep cells prior to their separation from the yolk-bed is readily comprehensible. In the case of other cells completely delimited, the

yolk-spheres must be taken up secondarily, as certainly happens in the case of the endoderm cells in much later stages, and if so, free yolk-spheres must be present in the disc, between the cells.

Study of the series confirms this assumption (Pl. V, fig. 27, *gp.*), though in the sections it is often difficult to be certain whether a particular group of yolk-spheres is really intercellular or situated in the periphery of a tangentially cut cell.

Below the greater part of the central region the deep cells are clearly marked off from the yolk-bed, and the under-surface of the disc presents a smooth, even contour, easily traceable despite the fact that the yolk-membrane is distinctly recognizable in only a few sections, one of which is depicted in Pl. V, fig. 27; but for a variable distance outwards from the central region the disc in many sections lacks a continuous boundary line, and here deep cells are to be found open to the yolk, whilst the yolk-spheres are free to spread up between and around the cells. This region of continuity between disc and yolk-bed, although discontinuous and subject to marked variations in width, forms a kind of junctional region, well seen in Pl. IV, fig. 26 and Pl. V, fig. 27 (*gp.*). Its variability in width is correlated with the marked variations in the degree of inward extension of the yolk-membrane below the peripheral region of the disc. Although this membrane is little prominent below the central region, in the peripheral region it is perfectly distinct in many of the sections (Pl. IV, fig. 25, *ym.*), though it varies greatly in width from section to section, and even on opposite sides of the same section, and may be absent on one or other side.

The cells forming the actual periphery of the disc, which is one cell thick, are mostly of medium size, and are usually rich in yolk-spheres. Many of them are well isolated from the yolk-bed (Pl. IV, fig. 25, *pdc.*), others are still open below. One very large peripheral cell seems to be a persisting marginal. It measures in diameter  $0.072 \times 0.027$  mm., and possesses two nuclei, one large ( $0.016 \times 0.0075$  mm. in diameter), the other quite minute. The lower half of the cell is occupied by a localized group of medium-sized yolk-spheres, whilst sparse finer spheres lie below its upper surface. The cell is still in continuity with the yolk-bed over a small area of its under-side.

Within the periphery, the disc is one to two cells thick. The cells tend to be large and are rich in medium-sized yolk-spheres (Pl. IV, fig. 25). Many of them are open to the yolk (Pl. V, fig. 27).

Eleven disc-cells have been observed in mitosis. Of these eight are superficial cells (in three the division-plane is vertical, and in two parallel to the surface), and three are deep cells.

*Vitellocytes.*—The vitellocytes in this stage are not only numerous but have undergone a noteworthy transformation into active-looking elements, with large plasma-rich cell-bodies, frequently produced into long pseudopodial-like processes, in marked contrast to the small inactive-looking cells present in the two preceding stages.

The peripheral vitellocytes (Pl. IV, figs. 25 & 26, *pv.*) mostly occur in fairly close proximity to the margin of the disc, though they are met with as far out as 0.13 mm. beyond that. The large vitellocyte seen on the left in Pl. V, fig. 28 (*pv.*) has a length of 0.080 mm., and is binucleate. In this cell the cytoplasm exhibits a rather exceptional differentiation; in greater part it is finely granular



and deeply staining, but below it is clear and finely alveolar in character. The processes to the number of three or four which arise from its under-surface are composed of a filamentous prolongation of the denser cytoplasm, which is more or less completely invested by a thin layer of alveolar cytoplasm. The smaller vitellocyte to the right of the large one in Pl. V, fig. 28 possesses an elongated thin cell-body and a flattened nucleus, and appears to be in continuity with the larger one. Many of the vitellocytes are of this elongated form with processes arising from their extremities, and sometimes from their under-surfaces as well; others are shorter and plumper, with processes arising from their under-surfaces, and lying between and enclosing yolk-spheres. We have observed one very long vitellocyte, with a length of 0.10 mm. and a thickness of 0.006 to 0.009 mm., its nucleus measuring  $0.030 \times 0.006$  mm. in diameter. Another, 0.096 mm. in length and 0.010 mm. in thickness, is binucleate, and yet another, 0.090 mm. in length and possibly composite, possesses a very flattened nucleus ( $0.012 \times 0.003$  mm. in diameter) and what appears to be an irregular group of chromosomes. Somewhat similar groups have been observed in two other cases, but none of them is suggestive of normal mitosis.

In addition to the peripheral vitellocytes, there are present in this disc some 17 sub-marginal vitellocytes (Pl. IV, fig. 26, *smv.*). Most of them are situated close below the yolk-membrane of the peripheral region. They differ from the peripheral in that the cell-body is never elongated, but is plumper and more compact, and often irregularly stellate in outline, whilst the nucleus is small and rounded, and usually stains deeply. These cells vary in diameter from  $0.015 \times 0.009$  mm., nucleus  $0.006 \times 0.004$  mm. to  $0.027 \times 0.015$  mm., nucleus  $0.007 \times 0.006$  mm. One exceptionally large cell with a diameter of  $0.042 \times 0.018$  mm. possesses a normal-looking compact group of chromosomes (prophase). This is the only instance of the possible occurrence of a normal mitosis in a vitellocyte we have so far encountered. One vitellocyte, situated close below two peripheral disc-cells, is trinucleate (Pl. IV, fig. 26, *smv.*).

*Sub-disc cells.*—There are no deep sub-disc cells in the yolk-bed in this stage, so far as we have observed, nor have we been able to recognize any indubitable sub-disc cells close below the disc. Deep cells rich in yolk, and situated in the proximity of the lower limit of the disc and not yet delimited from the yolk-bed, we have regarded simply as deep disc-cells, though some of them may be sub-disc cells not yet fully incorporated into the disc.

LC 7 (C.25.7.30). (Pl. V, figs. 29 & 30.)

(Diameter of egg, 4.6 mm. (fresh), 5 mm. (in alcohol). Diameter of disc,  $0.51 \times 0.55$  mm. Thickness, 0.076 to 0.080 mm. Fixation, Bouin's Fluid.)

This disc is definitely in advance of LC 6, inasmuch as it is now over most of its extent sharply delimited from the yolk-bed. It is biconvex in section, and as in LC 6 lies in a well-defined, though shallow, saucer-shaped excavation in the yolk-bed at the upper pole of the egg (Pl. V, figs. 29 & 30).

The disc is about four cells thick centrally, and thins out at its periphery to one cell. Over by far the major part of its extent, right out to its periphery, it is marked off from the yolk-bed by a perfectly definite but very thin yolk-membrane,

against which the limiting membranes of the overlying cells may directly abut, or a very narrow cleft (occupied by a vacuolated coagulum, sometimes simulating fibrillar strands) may intervene between the two (Pl. V, figs. 29 & 30, *ym.*). This membrane continues out beyond the actual periphery of the disc to reach the under-surface of the zona-albumen layer, where it becomes continuous with the egg-membrane. It is not, however, perfectly continuous below the entire extent of the disc, since in the intra-marginal junctional region, as in LC 6, small gaps are present here and there through which yolk-spheres seem to gain direct access to the disc (Pl. V, figs. 29 & 30, *gp.*). There has been some displacement of yolk-spheres on to the disc in the junctional region during the preparation of the sections, but making due allowance for this, we are satisfied after careful study of the sections that free yolk-spheres do find their way into the disc through the gaps in question.

The disc-cells are slightly smaller than those of LC 6, 15 cells averaging in diameter  $0.038 \times 0.019$  mm., and their nuclei  $0.0097 \times 0.006$  mm., and in contrast with that stage, the great majority of the cells are now isolated from the yolk-bed.

Centrally the superficial cells, oval or oblong, tend to be flattened against the zona-albumen layer, and for the most part lie in close contact. They contain minute yolk-granules in variable numbers. Many of them are not vacuolated, others are vacuolated peripherally like the deep cells. The majority of the deep central cells, which are oval or rounded in form, are rich in yolk-spheres, mostly minute, and many of them are vacuolated peripherally, much more so than those of LC 6. The more peripherally situated deep cells are, on the whole, less vacuolated, and tend to be rich in fine as well as large yolk-spheres. Large yolk-rich cells are common in the junctional region. The cells forming the periphery of the disc mostly appear to be delimited, and may contain small as well as large yolk-spheres, though they are not specially rich in yolk.

Eleven disc-cells (seven deep, four superficial) were observed in mitosis.

In this disc we encounter for the first time small rounded or oval bodies (up to  $0.027 \times 0.018$  mm. in diameter), composed of a cytoplasmic matrix, densely crowded with fine yolk-spheres. They appear to be similar to the "yolk-balls" (megaspheeres) which occur in the sub-germinal cavity of the bird's egg. Peter (1934) has also observed large non-nucleated yolk-masses intercalated between the superficial cells in cleavage stages, and occasionally lying below the ectoderm in later stages in the Chameleon, but states they are not found in the Lizard. They are not yet numerous and usually lie close above the yolk-membrane (Pl. V, fig. 29, *ybl.*). They arise as bud-like projections from the surface of the yolk-bed, which eventually become free. In later stages, these yolk-balls are met with in increasing numbers, and some of them attain a considerable size. They are evidently of importance as a means of providing the disc-cells with a supply of fine yolk, after the differentiation of the yolk-membrane.

*Vitellocytes.*—The peripheral vitellocytes call for no detailed description. They are similar to those of LC 6 and are quite well developed. They occur as far out as 0.08 mm. from the disc-margin.

We have counted some 24 sub-marginal vitellocytes. They usually lie in close contact with the under-surface of the peripheral portion of the yolk-membrane, though they may occur up to 0.10 mm. within the disc-margin. Several of them are binucleate.



*Sub-disc cells.*—Apart from three small eosinophil bodies, situated in the yolk-bed (one of them 0.081 mm. below the disc), which may be very degenerate nuclei, no deep sub-disc cells have been observed in this egg.

Although this disc is in advance of LC 6 in its all but complete delimitation from the yolk-bed, it seems to be exceptional in this respect, and it does not fit in so well as that stage does with the immediately succeeding discs of Group II. In LC 6, the cells are larger than those of LC 7, and many of its peripheral cells are still open to the yolk, as is generally the case in the earliest discs in Group II, whereas in LC 7, the majority of them are already delimited.

### *Appendix to Group I.*

#### B.15.7.30. (Pl. V, figs. 31 & 32.)

(Diameter of egg, 4.6 mm. (fresh). Diameter of disc, about  $0.48 \times 0.55$ – $0.65$  mm. Thickness, 0.043–0.051 mm. Shell, 0.006 mm. in thickness. Fixation, Bouin's Fluid.)

The disc of this egg is described in our notes as "very small, ill-defined, probably abnormal," and examination of the sections confirms that it is abnormal and that its periphery (so far as that can be observed) is poorly defined, but it is by no means small, as the above measurements show. Its peripheral region has suffered some damage in preparation, but otherwise the sections are good. Its aberrant features are deserving of brief description.

In its stage of development this disc seems to approximate most nearly to LC 5, but it diverges considerably from it in various points of detail. Its central region is about 4 cells thick and is more extended but thinner than in LC 5, and its under-surface is on the whole rather better defined and less irregular than in the latter, though the appearance of the disc varies greatly from place to place in the series. In some sections through the peripheral region of the disc, on one side, the deep cells are clearly delimited below, and the disc as a whole possesses a more or less well-defined plano-convex form (Pl. V, fig. 31), but in other sections more centrally situated, only odd cells or small groups of two or three cells are marked off from the yolk-bed, so that the under-surface appears quite irregular and devoid of a definite contour. The yolk-membrane is only occasionally recognizable and the lower limit of the disc appears to be defined simply by the line of contact of the yolk-free cytoplasm of the deep cells with the yolk-bed.

The central region in some of the sections presents much the same appearance of stratification that we noted in LC 5 (Pl. V, fig. 31, right side), the superficial cells and those immediately below tending to be flattened and closely packed together. The majority of the deep cells, however, are plump, oval and plasma-rich, little if at all vacuolated and devoid of yolk, but intermingled with them, there are present numbers of larger cells rich in small as well as large yolk-spheres (Pl. V, fig. 31), whilst amongst the deep cells resting on the yolk-bed, smaller yolk-laden cells are present which may or may not be delimited from the latter.

The peripheral region of the disc is noteworthy for the variability in the constitution of its marginal portion. In many of the sections the latter is formed over a width of up to three or four cells, of large, oval or rounded cells, poor in cytoplasm and crowded with coarse and fine yolk-spheres (Pl. V, fig. 31, *yc.*), many of them open to the yolk. Cells of this coarsely yolk-laden type occur nowhere else in Group I, and are clearly not normal.

The cells forming the actual margin of the disc, so far as we have been able to observe them, are also extremely variable, ranging as they do from small cells, round about  $0.03 \times 0.015$  mm. in diameter and containing sparse fine yolk-spheres, to quite large cells, up to  $0.048 \times 0.030$  mm. in diameter, laden, like those mentioned above, with large and small yolk-spheres.

The most striking peculiarity in this disc remains to be mentioned. Unlike the normal disc, which suffers a gradual reduction in width and in thickness as its margin is approached, the present disc, though it becomes reduced in width, rather suddenly increases in thickness to 0.066 mm. just before it terminates (Pl. V, fig. 32). The thickened region is seen in the figure to be roughly triangular in

outline and to project down into the yolk of the marginal zone. It is about four cells in depth. The cells composing it are oval or rounded in form and relatively large, their diameters varying from  $0.018 \times 0.015$  mm. to  $0.025 \times 0.021$  mm. They possess plasma-rich cell-bodies and deeply staining nuclei, are only slightly vacuolated and are mostly devoid of yolk. The thickening has evidently resulted from a localized hypertrophy of the disc-cells, especially of the deep cells which seem to have increased in number as well as in size.

*Sub-disc cells.*—These cells (Pl. V, fig. 31, *sdc.*) are exceptionally numerous in this disc. They number about 24, and are all situated in more or less close proximity to the lower limit of the disc. They measure up to  $0.033 \times 0.018$  mm. in diameter and are very variable in their nuclear constitution, eight of them being uninucleate, seven binucleate and the remaining nine each possessing from three to seven nuclei.

*Vitellocytes.*—The vitellocytes, so far as we have been able to observe them, are poorly developed and not very normal looking, their cytoplasm being pale staining and eosinophil. Several of them are binucleate, one is trinucleate, and in another the nucleus appears to have fragmented.

From the structural characters of this disc it appears altogether unlikely that it would have given origin to a normal embryo.

### SUMMARY AND DISCUSSION OF LATER CLEAVAGE STAGES (LC 1–7).

A survey of the meroblastic cleavage process in the later blastodiscs (LC 1–7) comprised in Group I shows that the division of the blastomeres follows no very regular plan, and that in the earlier members of the Group there is often a considerable time-lag between nuclear and cytoplasmic division.

In the two earliest blastodiscs here dealt with (LC 1 and 2), the blastomeres exhibit the same characteristic arrangement into a central group and an enclosing marginal ring as in the 31- and 32-celled stages (CF and CG) previously described in Part IV. But, whereas in the latter, the blastomeres form a single layer, and all of them are in open continuity with the yolk-bed, here some of them have become closed off or delimited from the yolk, and deep-seated cells have begun to appear, thus heralding the commencing transformation of the one-layered disc into the several-layered or stratified disc of later stages.

Delimitation of the blastomeres from the yolk is not the result of cell-division in the horizontal plane, but is due to a spontaneous rounding off or constriction affecting the region of continuity of the cytoplasm of the cell-body with the cytoplasmic reticulum of the yolk-bed.

The central blastomeres, somewhat more flattened and more ovoidal in form than in stages CF and CG, may divide after or before they become delimited from the yolk. In the former case, the blastomere may divide in the vertical plane to furnish two superficial cells, or in the horizontal plane to form a superficial cell and a deep cell. In the latter case, in the earlier blastodiscs, division usually appears to be effected in a plane more or less oblique to the surface, and is slightly unequal. It results in the formation of a larger superficial cell and a smaller deep, which tends to lie not directly below its sister-cell but obliquely thereto. Both may remain for a time in continuity with each other and with the yolk-bed, or they may separate completely from each other, only the deep cell remaining open to the yolk.

The delimitation of the deep cells from the yolk-bed sets in relatively late (first in LC 4) and affects, in the first instance, the cells in the central region of the disc. But it seems highly probable that some of them divide prior to their delimitation, the uppermost of the two daughter-cells rounding off and forming



a deep disc-cell, the lowermost remaining open to the yolk, and even sinking down into it, or it may itself divide like the parent cell. We think the cells which are met with for the first time in the yolk-bed of stage LC 4, and which we have termed "sub-disc cells," originate in this way. Those of them which remain close below the disc may eventually become delimited and incorporated in it, much as happens in the so-called "Nachfurchung" process in the Reptilian blastodisc (Virchow, 1892; Will, 1895). Others which migrate more deeply into the yolk-bed may help to form the free cells and nuclei that occur sporadically and in very varying numbers in the yolk-bed in later stages, though the great majority of these "yolk-bed cells and nuclei," as we have termed them, would seem to be derived from inwandered sub-marginal vitellocytes.

It is suggested that the sub-disc cells as well as the vitellocytes correspond to the free cells variously known as merocytes, merocyte nuclei, periblast cells, yolk-nuclei, etc., which occur in the yolk-bed in the Reptilian and Avian egg (*v. p.* 20).

The structural distinction between marginal and central blastomeres is soon lost (already in LC 3), the marginal cells being used up in the production, on the one hand, of peripheral and central disc-cells, and on the other, of peculiar and highly characteristic cells which we have termed "vitellocytes," possessed of migratory properties and the capacity of sending out pseudopodial processes and of enclosing yolk-spheres. They lie at first just outside the periphery of the disc, in the yolk of the marginal zone and immediately below the egg-membrane, but, whilst some of them remain in this position, others wander outwards below the egg-membrane, away from the disc, and yet others migrate inwards below the yolk-membrane to underlie the margin of the disc (sub-marginal as contrasted with peripheral vitellocytes). Vitellocytes have already appeared in the 41-celled stage (LC 1).

In succeeding stages they increase in number by division, and are destined eventually (in stage VVH 35 of Group III) to fuse together to form a continuous band-like ring of nucleated cytoplasm which encircles the disc and extends inwards for a very short distance below its periphery. This ring constitutes the germ-ring, as we have termed it. It is a structure of the first developmental importance, since it conditions the growth in surface-extent of the blastodisc and its concomitant transformation into a thin blastoderm capable, under its continued influence, of growing round to enclose the yolk-mass of the egg.

We have already referred (*ante*, p. 20) to the observations of Virchow (1892) and Will (1895) on the yolk-cells which condition the post-cleavage process in *Lacerta*, but some further reference to them may be made here.

Virchow originally described the occurrence in the yolk underlying the early blastoderm, of two varieties of yolk-cell, viz., plasma-poor cells and plasma-rich cells and to designate them, adopted the term merocyte, first used by Rückert (1885). His observations have been largely confirmed by Will.

The plasma-poor cells occur exclusively in the yolk underlying the embryonal shield and the surrounding area intermedia of the blastoderm, *i.e.*, in the floor of the sub-germinal cavity. They appear like "free nuclei" in the yolk, being devoid of an obvious protoplasmic body, though as Virchow (92 *a*) points out, they must be surrounded by some protoplasm. Sometimes there are traces of a yolk-

free area around them, but usually the yolk-granules abut directly on the nuclear membrane (92 *a*, fig. 22, Pl. 10). These cells are the main participants in the post-cleavage process which Virchow states is more active and more resembles the typical cleavage process, below the peripheral part of the blastoderm than elsewhere.

The plasma-rich cells are exclusively situated below the region of the germ-wall as well as in the region of the superficial yolk surrounding the same. In Virchow's own words (92 *b*, p. 52), "*Ihr typischer Platz ist unter der distalen Zone des Randwulstes, doch reichen sie zuweilen bis zum Randsaume selbst, ja etwas über denselben hinaus*" (italics ours). The cells possess a well-marked cell-body containing one or more nuclei; they are usually spherical or elliptical in form and of large size. The cytoplasm of the cell-body, according to Virchow (92 *a*, fig. 20, Pl. 10), is distinguishable into a perinuclear dense, yolk-free zone and a peripheral zone in the form of a network of fine fibrils. These latter penetrate between the neighbouring yolk-granules and also serve to connect adjacent cells; in his own words "*benachbarte Merocyten stehen durch die Protoplasmafäden ihres Randes in Verbindung*" (92 *a*, p. 195).

The figures provided by Will of these cells (see especially his fig. 28 <sup>c</sup>, Pl. 4 and fig. 28 <sup>p, n, and o</sup>, Pl. 5) clearly show that they are provided peripherally with numerous short, delicate cytoplasmic processes. Curiously enough, Will does not describe them as such, nor does he refer to Virchow's observations, but simply states that the cells are in direct continuity at their peripheries with the cytoplasmic network in the yolk. Possibly, what we take to be processes, he regarded as parts of the latter, but that they are genuine processes is shown by the fact that they can anastomose with those of an adjacent cell and so serve to connect the cells as Virchow describes, and as is clearly seen in his fig. 28 <sup>n</sup>, Pl. 5, where a large cell containing four nuclei is thus connected with a small uninucleate cell.

Virchow states that, since cells transitional in character between the plasma-rich and plasma-poor cells occur, the latter must be regarded as two varieties of the same cell-type.

In their general characters, their position, below and around the margin of the blastoderm, and their structural relationship to each other and to the cytoplasmic reticulum in the yolk, these plasma-rich yolk-cells in the Reptile so strikingly resemble the vitellocytes of the Monotreme that it is difficult to avoid the conclusion that in them we have the fore-runners out of which the more highly specialized vitellocytes have been evolved; and if that be so, then the further conclusion follows that just as the plasma-rich and the plasma-poor cells are two related varieties of cell, both presumably derived from cleavage-cells and respectively peripheral and central in disposition, so also are the vitellocytes and the sub-disc cells in the Monotreme, two related cell-types, the former undoubtedly derived from marginal cleavage-cells and the latter almost certainly from central blastomeres.

In the earlier stages, under review, the superficial cells increase in number much more rapidly than the deep; in LC 4, for example, the former number about 44 and the latter about 12, but in the interval between LC 4 and LC 5, the deep cells as well as the superficial have undergone division so actively that in LC 5 the disc in its central region has attained a thickness of about 4 cells, thinning out peripherally to a thickness of two cells and to one at the margin. Except



over a very restricted area below the central region, the under-side of the disc in LC 5 is still very irregular and lacks a definite contour, many of the deep cells being still open to the yolk.

In the succeeding stages, however, the delimitation of the deep cells is seen to have made rapid progress, and concomitantly the under-surface of the disc over the major portion of its extent has acquired a smooth, even contour, to which the upper surface of the yolk-bed conforms. This is due to the circumstance that as soon as a few contiguous deep cells have become delimited, a thin pellicle-like limiting membrane (the yolk-membrane) is differentiated on the surface of the bed, no doubt through the agency of its cytoplasmic reticulum. The yolk-membrane first appears in LC 5 below a restricted area of the central region of the disc, and in LC 6 it has also been established in places below its periphery, whilst in the last member of the Group (LC 7), it has been completed all over the surface of the yolk-bed, except that in the intra-marginal junctional region there are still present occasional gaps through which yolk-spheres appear to gain direct access to the disc and where deep cells are still open to the yolk (LC 6).

In the peripheral region also, where the disc is one-cell thick, more (LC 6) or fewer (LC 7) of the cells there situated likewise remain open to the yolk.

In all the later discs many of the cells (both superficial and deep), especially in the peripheral region, are rich in secondarily included yolk-spheres. The utilization of the yolk of the yolk-bed by the growing blastomeres (apart from that originally included in the cells prior to their delimitation) first becomes noticeable in LC 3, and becomes gradually more marked in the later discs, the blastomeres apparently ingesting the free spheres which penetrate in between them, especially in the peripheral region of the disc. Whether the vacuolated central region of the yolk-bed, overlying its junction with the lateral neck, forms an active centre for yolk-digestion, we are unable to determine, though its appearance is suggestive of some such activity.

The completed blastodisc, which has become delimited from the yolk-bed in the way described, appears in the most advanced members of the Group (LC 6 and LC 7) as a more or less compact mass of cells, circular in outline and biconvex lens-shaped in section, which attains a thickness of about four cells centrally and thins out to the thickness of a single cell at its periphery. In the marginal zone of the yolk-bed around the latter, there are present considerable numbers of vitellocytes (peripheral and sub-marginal). The disc rests in a shallow, saucer-shaped depression in the yolk-bed at the upper pole of the egg, and measures just over 0.50 mm. in diameter and about 0.080 mm. in maximum thickness. It presents no trace of bilateral symmetry or polarity; the polarity recognizable in the unsegmented disc and in the 4- and 8-celled cleavage stages having become entirely obscured by the time the 32-celled stage is reached, as we have recorded in Part IV (*v. p.* 571). In the Chameleon, Peter (1934) states that the cleavage disc is also devoid of any trace of bilateral symmetry or polarity.

Whilst the meroblastic cleavage process in the Monotreme conforms in its broad outlines to that in the Reptile, as witness for example the comparable grouping of the blastomeres in the early blastodisc into marginal and central, and the occurrence in both of free cells in the yolk below and around the blastodisc, there are certain deviations to be noted, *e. g.*, the extremely belated appearance of the

sub-germinal cavity in the Monotreme, if we can regard the sub-blastodermic space which we describe in *Platypus* SS of Group V as such (v. p. 93), the great reduction in the post-cleavage process, and the absence in the Monotreme of any pronounced thickening of the marginal region of the blastodisc to which the term germ-wall (of Will & Peter) can be applied. Whether or not this absence can be correlated with the eventual presence of the nucleated syncytial germ-ring round the periphery of the Monotreme blastodisc, cannot be decided until the significance of the marginal cytoplasmic zone (v. pp. 105–109), which in the Reptile occupies the site of the germ-ring, has been established.

#### GROUP II.

In this Group we have included seven blastodiscs of *Echidna* and two blastodiscs of *Platypus* from twin-eggs (B and BB). Of the former, four, viz., VVH 36, 17, 37, and 41, are specially important. They form a progressive developmental series of which the earliest member, VVH 36, links up without difficulty, though perhaps not very closely, with LC 6 and 7 of Group I, whilst the most advanced member, VVH 41, immediately precedes the earliest stage, VVH 35, in Group III.

The Group marks the culmination of the cleavage process and the attainment by the blastodisc of what we may regard as its completed condition. The blastodiscs show a progressive increase in the number of their constituent cells as we pass from the earliest stage (VVH 36, with about 70 surface-cells) to the most advanced member of the Group (VVH 41, with about 220 surface-cells), but otherwise they are very similar in their general form and structure, so much so that in our preliminary survey of the material we grouped them together as the "button" stage. The disc, in section, appears typically as a compact rather massive-looking formation, relatively thick and plano- or bi-convex in form. It occupies a well-marked concavity, floored below by the yolk-bed from which it is sharply delimited, except here and there in the intra-marginal junctional region and at its periphery.

The blastomeres are large, oval or rounded in form, are often vacuolated, and in the peripheral region of the disc especially, are rich in yolk-spheres.

It is in this Group that the blastomeres, as the result of their active assimilation of yolk, attain their maximum size (average diameter in VVH 36,  $0.048 \times 0.039$  mm.), and the disc its maximum thickness (0.16 mm. in VVH 17).

Whilst the blastodiscs in this Group are notably thicker than those of Group I, they show no significant increase in diameter over those of the latter, the largest disc in the Group, that of VVH 41, having a diameter of  $0.55 \times 0.50$  mm. as compared with the largest in Group I, LC 7, with a diameter of  $0.55 \times 0.51$  mm. As we shall see, growth in surface-extent of the blastodisc and its concomitant conversion into a blastoderm, is conditional on the establishment of the germ-ring, and that all-important event is not initiated until we reach the stage represented by egg VVH 35 of Group III.

#### VVH 36. (Pl. VI, figs. 33–35.)

(Diameter of egg, 4 mm. (fresh), 5.29 mm. (after fixation), and of ovum,  $4.4 \times 4.1$  mm. Diameter of disc,  $0.38 \times 0.46$  mm. (from the sections). Thickness, 0.128 mm. Fixation, FBA.)



A surface view of the disc is shown in Pl. VI, fig. 33, and should be compared with Pl. II, fig. 13 of LC 3. The disc is small, and its most striking feature is the very irregular contour of its peripheral region. From the figure it will be seen that the superficial cells in the central region are of fairly uniform size, and smaller on the whole than those in its peripheral region, which are more variable in size, the largest cells being at the periphery. These peripheral cells exhibit no regularity in their disposition, with the result that the disc presents a very irregular peripheral contour, which is much accentuated by the presence immediately outside the disc-cells of a number of cell-like areas, mostly rather ill-defined and devoid of definite boundaries on their outer sides. These areas, about 12 in number, are suggestive of the occurrence of a transitory cleavage in connection with the vitellocytes, of which there were indications in LC 1 (p. 12), and this seems to be confirmed by study of the sections.

A count of the cells visible in the surface view indicates that the superficial layer is composed of from about 70 to 73 cells, whilst an enumeration of the same cells in the sections yields the figure of 71. The number of deep disc-cells is about 57, so that the total number of cells composing the disc is about 128.

The sections show that the surface of the disc in the central region is fairly smooth and even, with the superficial cells lying for the most part in close apposition and marked off from each other by superficial grooves, mostly quite shallow (Pl. VI, fig. 34). In the peripheral region the surface tends to be more uneven, and occasional gaps are present between the cells (Pl. VI, fig. 35).

In section (Pl. VI, fig. 34), the disc presents a characteristically compact appearance and a plano-convex form, but it is not radially symmetrical all over, as may be seen from the figure, where on the right side it thins out to the thickness of a single cell, over a width of three cells, whereas on the left it terminates much more abruptly in the peripheral cell (*cf.* also Pl. VI, fig. 35).

The disc-cells have now attained a large size, the average diameter of 24 cells measured being  $0.048 \times 0.039$  mm., and that of 12 nuclei  $0.012 \times 0.010$  mm., the cells ranging in diameter from  $0.037 \times 0.036$  to  $0.057 \times 0.045$  mm., and the nuclei, from  $0.010 \times 0.009$  to  $0.013 \times 0.012$  mm.

Centrally the disc reaches a thickness of four cells. The superficial layer is distinct and composed of rounded, oval or oblong cells, rich in cytoplasm, which is densely and finely granular and only slightly vacuolated. Some of them contain localized groups of fine yolk-spheres. The deep cells are very similar, but are more vacuolated and richer in fine yolk-spheres.

In the peripheral region the cells are on the average larger than the central, and are much richer in yolk, many of them containing small yolk-spheres as well as fine, which are often localized in one area of the peripheral zone of the cell. Three binucleate cells were observed in the peripheral region, all rich in fine yolk-spheres, one of them superficial and very large ( $0.080 \times 0.048$  mm. in diameter), one deep and one at the margin of the disc.

The actual peripheral cells are always yolk-laden, and many of them are open to the underlying yolk (Pl. VI, fig. 34, *pd.*). A number of the deep cells in the peripheral region are also still open, whilst over a small area below the periphery and extending through three sections the yolk-membrane is absent and the disc is open to the yolk (Pl. VI, fig. 34, *gp.*). Otherwise the disc is sharply delimited

from the yolk-bed, the yolk-membrane being distinct both below the disc and beyond its periphery.

Numbers of small yolk-balls (Pl. VI, fig. 34, *ybl.*) are present between the deep disc-cells and in contact with the surface of the yolk-bed, some of them being still connected with it.

No sub-disc cells were observed.

*Vitellocytes.*—These cells are well developed, and though they are mostly small, some few of them reach a large size (up to  $0.060 \times 0.027$  mm. in diameter, nucleus  $0.018 \times 0.012$  mm.). Their cytoplasm, in contrast with that of the disc-cells, is not obviously granular, and both it and the nucleus stain a dull red tint with eosin, in place of the bright red of the disc-cells.

They number about 37. Of these four are sub-marginal and one lies 0.03 mm. below the yolk-membrane, just outside the disc-periphery.

The remainder lie at varying distances from the latter (up to 0.13 mm.), and are mostly situated superficially close below or in intimate contact with the egg-membrane. Altogether about 15 vitellocytes lie close to, and on a level with, peripheral disc-cells, and of these ten with their related yolk-spheres form more or less marked convex projections on the surface, with a width in two instances of 0.045 mm., and in another of 0.061 mm.

Five of the ten abut directly on peripheral disc-cells, a shallow surface groove indicating the limit between them (Pl. VI, fig. 35, *pv.*); but we have encountered one case in which the vitellocyte is not marked off superficially from the disc-cell it adjoins, and which is open to the yolk, the two together forming a common convexity, with a width of 0.072 mm.

In two instances we have observed two adjacent vitellocytes with a superficial groove midway between them.

The appearances here described afford an explanation of the ill-defined cell-like areas visible around the disc in the surface view. They suggest that we have here to do with a transitory cleavage process, induced by the vitellocytes.

Some of these cells adjoining the disc-margin might easily be mistaken on superficial examination for peripheral disc-cells not yet delimited from the yolk. On the other hand, they might be regarded as affording evidence of the inclusion of vitellocytes in the disc. We may therefore refer to the cell seen in Pl. VI, fig. 35 (*pv.*) in a little more detail. In this figure, immediately to the left of the rounded peripheral cell (*pd.*) at the left edge of the disc and abutting on its cell-membrane, there is visible a cell (*pv.*) which forms a convex projection on the surface and is marked off from the peripheral disc-cell (*pd.*) by a shallow surface groove. Its cytoplasmic body (about  $0.024 \times 0.018$  mm. in diameter) gives off short radiating processes all round, which enclose yolk-spheres, there being a narrow zone of small spheres of varying diameter on its upper side bounded by the egg-membrane and similar spheres on its lower side which pass over without limit into the yolk of the marginal zone. Its cytoplasm stains a dull red colour with eosin, like that of undoubted peripheral vitellocytes, in contrast with the bright red staining of the disc-cells, and is not obviously granular as is that of the latter. The nucleus is large ( $0.015 \times 0.009$  mm. in diameter) and vesicular, with a poorly developed reticulum. Two other cells (one of practically the same size as that just described, the other slightly larger ( $0.030 \times 0.021$  mm. in diameter)



exhibit precisely the same relations and structure. From their characters we think these cells are unquestionably vitellocytes, and as to the possibility of their becoming included in the disc, all we can say is that this stage affords no positive evidence that this actually happens, and the same remark applies to two of the sub-marginal vitellocytes which produce convexities on the surface of the yolk-bed, covered by the yolk-membrane.

VVH 17. (Pl. VI, figs. 36-39 ; Pl. VII, figs. 40 & 41.)

(Diameter of egg, 4 mm. (fresh), 5.32 mm. (after fixation), and of ovum, 4.48 mm. Diameter of disc,  $0.450 \times 0.488$  mm. Thickness, 0.16 mm. Fixation, FBA.)

This disc, which is excellently fixed, is well in advance of VVH 36. Seen in section (Pl. VI, fig. 37), it is plano-convex in form, with a smooth even surface, and appears thick and compact. Apart from the atypical disc of VVH 4, it is the thickest disc in the Group II series, measuring 0.16 mm.

The surface view (Pl. VI, fig. 36) shows that the superficial cells are fairly regular in size and lie in close contact with each other, and in section they are seen to form a quite definite superficial layer (Pl. VI, fig. 37) as in VVH 36. In the surface view about 120 cells are visible, whilst a rough count of the nuclei in the sections yields the figure of 114. The periphery of the disc is more regular in contour than that of VVH 36, though still somewhat ragged owing to the presence of odd projecting cells.

Centrally the disc is from four to five cells in thickness (Pl. VI, fig. 37). It terminates somewhat abruptly at its periphery, where it is mostly one cell thick, though in a few places it is two cells thick. Over its central region it is marked off from the yolk-bed by a delicate but quite distinct yolk-membrane, and in a few of the central sections, it is possible to trace the latter continuously out below the disc-periphery into continuity with the egg-membrane. In the remainder, however, the yolk-membrane is interrupted over quite small, more or less disconnected areas below the peripheral region of the disc, on one or other side of the sections, occasionally on both sides, and here the deep disc-cells, open or closed, are in direct relation with the yolk of the yolk-bed.

The disc-cells are large, with correspondingly large nuclei (the average diameter of 24 cells measured being  $0.043 \times 0.036$  mm., and that of 12 nuclei  $0.012 \times 0.010$  mm.). They are compactly arranged, with only occasional clefts between them, often occupied by small yolk-balls. Their cytoplasm is finely granular, and in a number of the cells there is present in it, close to the nucleus, a dense homogeneous oval body (the centrosphere?),  $0.009 \times 0.006$  mm. or less in diameter.

The more superficially situated central cells are only slightly if at all vacuolated peripherally, and may contain sparse fine yolk-granules or none, and the same holds true for some of the deep cells lying adjacent to the yolk-membrane. Many of the more deeply situated central cells, on the other hand, are richly and finely vacuolated peripherally, the vacuoles containing numerous fine basophil granules identical with those in the central part of the yolk-bed. Such cells, when cut tangentially, present the clear vacuolated and finely dotted appearance well seen in Pl. VI, fig. 37.

In the peripheral region of the disc the cells, both superficial and deep, are much richer in yolk, small as well as medium sized spheres being present in their cytoplasm (Pl. VI, fig. 37). The actual peripheral cells (Pl. VI, fig. 39, Pl. VII, fig. 40, *pd.*) usually contain such spheres, and all but a few of them are delimited from the yolk of the marginal zone.

One peripheral cell is noteworthy in that it appears to have established connection with an adjacent vitellocyte (Pl. VII, fig. 41, *pd.*), and most precociously, since such connections are not normally formed until the germ-ring is laid down (*v. p.* 46). From the figure it will be seen that the cell-body of the vitellocyte (*pv.*) involved is curved, and that a slight irregular space is left between its curved surface, clothed by the yolk-membrane, and the body of the peripheral cell. This space is closed above by a finely vacuolated projection from the peripheral cell, which is attached to a slight ridge at the upper extremity of the vitellocyte, marking the junction of the yolk- and egg-membranes, whilst a second slighter connection is formed by a minute spike-like projection given off shortly below that first mentioned.

A fair number of disc-cells are in mitosis.

*Vitellocytes* (Pl. VI, figs. 38 & 39; Pl. VII, figs. 40 & 41, *pv.*, *smv.*).—These cells in this disc are numerous, very well developed, and excellently preserved. The peripheral vitellocytes number about 51, of which ten are binucleate, one trinucleate, and the remainder uninucleate. The sub-marginal vitellocytes (Pl. VI, fig. 39, *smv.*) number about 26, of which two were observed to be binucleate.

Rather more than half of the peripheral vitellocytes are located close to the margin of the disc, and here they are mostly large. One such cell (Pl. VII, fig. 40, *pv.*) attains a diameter of  $0.090 \times 0.022$  mm. and is binucleate, one nucleus measuring  $0.015 \times 0.012$  mm. in diameter, the other slightly less. The remainder of the peripheral vitellocytes lie at varying distances from the disc-margin (one as far out as 0.18 mm.) and are mostly small and attenuated, with flattened nuclei.

The sub-marginal vitellocytes are situated as usual below the peripheral region of the disc, in close relation to the yolk-membrane (Pl. VI, fig. 39, *smv.*), whilst a few lie in or adjacent to the gaps in the latter, in the junctional region. They do not occur below the central region of the disc.

The cell-bodies of the vitellocytes are extremely irregular in form, produced as they are into processes varying in number and in thickness, but mostly thin and tapering. They are relatively rich in cytoplasm which stains a rather duller tint with eosin, and is more finely granular than that of the disc-cells. Their nuclei, mostly oval or rounded, are large (up to  $0.016 \times 0.012$  mm. in diameter) and active-looking. Apart from the yolk-spheres enclosed by their processes, small spheres are occasionally present in their cytoplasm as well as sparse, minute yolk-granules below their upper surfaces.

All but a very few of the peripheral vitellocytes (one of the few is seen in Pl. VI, fig. 38 (*pv.*), and is possibly on the way to becoming sub-marginal) occupy a superficial position, their upper surfaces being closely adherent to or fused with the egg-membrane, which is still distinguishable as a very thin line on the surface of the cytoplasm, and they must also have incorporated the subjacent portions of the extremely attenuated film-like layer of cytoplasm (the remains of the peripheral



cytoplasmic layer of the oocyte) which underlies the egg-membrane and in which minute yolk-granules are situated.

The processes given off from the vitellocytes run between the yolk-spheres abutting on their cell-bodies, and rapidly thinning, anastomose with each other to form a well-marked reticulum, often with fine yolk-granules in its strands, in the meshes of which the yolk-spheres lie enclosed (Pl. VI, fig. 38; Pl. VII, figs. 40 & 41, *cre.*). This reticulum continues into an even more delicate and more irregular cytoplasmic network which extends fairly deeply into the marginal zone as well as inwards, below the disc, into the yolk-bed proper. It might be concluded that the whole of it is derived from the vitellocytes, and that these have the subsidiary function of "organizing" the yolk of the marginal zone, and certainly it is most obvious in the superficial part of the zone. But it has to be remembered that the yolk-bed, including the marginal zone, is permeated by a very fine cytoplasmic network of its own, and it may well be that the marginal reticulum is of two-fold origin, its more superficial part being furnished by the vitellocytes and its deeper part by the intrinsic network of the yolk-bed.

As regards the question of the inclusion of vitellocytes in the disc, so far as the peripheral vitellocytes are concerned, there is not the slightest indication of any such happening, nor, we may add, of the occurrence in this egg of a transitory cleavage in connection with them. As concerns the sub-marginal vitellocytes, all we can say is that a few cells, which from their characters appear to be vitellocytes and not simply deep disc-cells not yet delimited, occupy positions in the gaps in the yolk-membrane in the junctional region where they might easily become included in the disc, but we have no evidence that this actually does happen.

#### VVH 37. (Pl. VII, figs. 42 & 43.)

(Diameter of egg, 4.5 mm. (fresh), 5.7 mm. (after fixation), and of ovum, 4.7 mm. Diameter of disc,  $0.50 \times 0.52$  mm. Thickness, 0.13 mm. Fixation, FBA.)

The surface view of this disc (Pl. VII, fig. 42) shows that some progress has been made, compared with that of VVH 17. The number of superficial cells has increased to about 153; the cells are more uniform in size, though there are still some larger cells round the periphery, and the latter is acquiring a more regular contour.

The disc centrally is four cells thick, and thins out peripherally to a thickness of one cell, over a width varying from one to two cells. It is a little thinner than that of VVH 17, its thickness being 0.13 mm. as compared with 0.16 mm. in the latter, and the cells are very slightly smaller, the average diameter of 24 measured being  $0.042 \times 0.034$  mm., and that of 12 nuclei  $0.011 \times 0.099$  mm.

A superficial layer, composed of oval, oblong or rounded cells, is present (Pl. VII, fig. 43), but is not quite regular, shallow surface-furrows and occasional gaps occurring between the cells. Spaces also occur between the deep cells, and in these yolk-balls up to  $0.030 \times 0.024$  mm. in diameter are present in considerable numbers.

The superficial cells over the central region as a whole are poor in yolk and little vacuolated, though here and there a vacuolated yolk-rich cell is met with (Pl. VII, fig. 43). The deep cells also vary in their yolk-content, some contain little, others are laden with peripherally situated spheres. Many of the cells, like

those of VVH 17, possess a small irregularly oval mass of condensed cytoplasm close to the nucleus.

In contrast to the more central cells, the majority of the peripheral cells of the disc over a width of several superficial cells are richly laden with fine to medium-sized yolk-spheres, identical with those in the peripheral part of the yolk-bed.

The disc, in sections passing through its central region, is seen to be well delimited from the yolk-bed, the yolk-membrane being clearly marked and frequently separated from the deep disc-cells by a narrow space. Over about one-half of the disc, curiously enough, the delimitation is nearly complete, but over the remainder there are isolated areas, with a width of about 0.10 to 0.12 mm. below the peripheral region, where large, yolk-laden, deep disc-cells are open to the yolk-bed, whilst isolated cells, richly yolk-laden and up to  $0.068 \times 0.048$  mm. or more in diameter, are to be met with, likewise open to the yolk-bed. Three such cells are binucleate and one similar cell, but delimited, is also binucleate, the load of yolk having evidently hindered cytoplasmic division.

The actual peripheral disc-cells (Pl. VII, fig. 43) vary in diameter from  $0.042 \times 0.032$  mm. to  $0.064 \times 0.052$  mm. They contain yolk-spheres, and are mostly delimited.

*Vitellocytes*.—Peripheral vitellocytes are numerous; they are for the most part small, and lie either in contact with the egg-membrane or shortly below it, close to the margin of the disc, though one occurs 0.16 mm. from the disc-margin. Three at least are binucleate, whilst five are in process of mitosis, one of them in the metaphase having apparently two groups of chromosomes at one pole of the mitotic figure.

In addition some 21 or more sub-marginal vitellocytes are present below the periphery of the disc. They are small, though one attains a diameter of  $0.027 \times 0.015$  mm., is situated shortly below the yolk-membrane, 0.18 mm. within the margin of the disc and is trinucleate (Pl. VII, fig. 43, *smv.*).

There is no evidence of the incorporation of vitellocytes in the disc.

VVH 41. (Pl. VII, figs. 44 & 45; Pl. VIII, fig. 46.)

(Diameter of egg (fresh) 4.5 mm., and of ovum, 4.7 mm. Diameter of disc,  $0.55 \times 0.50$  mm. Thickness, 0.128 mm. Fixation, FBA.)

This is the most advanced of the discs included in Group II, and shows us the condition of the disc when it has attained its maximum development prior to the appearance of the germ-ring.

In surface view (Pl. VII, figs. 44 & 45), the disc presents a much more ragged and irregular contour than that of VVH 37 owing to the presence of out-jutting cells and groups of cells. Over its central region the surface-cells are more closely arranged and more uniform in size than in the peripheral region, where occasional gaps occur between them, and cells larger than the average central cell are present, especially at the disc-margin. In the figures the disc is seen to be surrounded by a dark marginal zone, wider on one side than on the other. In section this zone has a width on one side of approximately 0.28 mm., and on the other of about 0.22 mm., whilst its maximum depth is about 0.064 mm. It is formed mainly of small yolk-spheres which continue inwards below the disc-margin into those of the yolk-bed proper.



The number of superficial cells visible in Pl. VII, fig. 45 is about 220, a definite increase on VVH 37.

The disc centrally is five to six cells in thickness (Pl. VIII, fig. 46). The disc-cells, oval or rounded in outline, are definitely smaller than those of VVH 37, the average diameter of 24 cells being  $0.030 \times 0.025$  mm., and that of their nuclei  $0.0093 \times 0.0090$  mm.; but the increase in the number of the cells has generally maintained the thickness of the disc, which is only very slightly below that of VVH 37 (0.128 mm. as compared with 0.13 mm. in the latter). There has evidently been considerable mitotic activity in the disc-cells, and cells in division are still met with.

The sections show that the surface-cells form a rather loose, somewhat irregular superficial layer, occasional gaps occurring between them, especially in the peripheral region, whilst the deep cells are also loosely arranged, small yolk-balls being present in the intervening spaces (Pl. VIII, fig. 46, *ybl.*). In the central region many of the cells are coarsely vacuolated, but they are relatively poor in yolk, containing only sparse fine spheres, though here and there amongst the small cells larger cells (up to  $0.058 \times 0.044$  mm. in diameter) are met with which are much more vacuolated and rich in coarser spheres. In the peripheral region the cells, both superficial and deep, tend to be richer in yolk than the central, many of them being greatly vacuolated and laden with medium sized spheres. The large peripheral cells visible in the surface view attain diameters of from 0.052 to 0.064 mm.; they are also vacuolated and rich in medium sized and small spheres. Some of these large cells are in open continuity with the yolk-bed, and a few of the deep cells in the peripheral region are also open. But apart from these cells the disc is clearly marked off from the yolk (Pl. VIII, fig. 46). Where out-juttings occur at the periphery they are one cell thick and a few cells in width.

On the whole, the yolk-content of the disc-cells in this egg is less than in VVH 37.

In addition to small yolk-balls, there occur in this disc a few quite large balls (one visible in Pl. VIII, fig. 46, *ybl.*, reaching a diameter of  $0.064 \times 0.048$  mm.). They are greatly vacuolated and rich in small spheres of varying size, and might easily be mistaken for large disc-cells. We have encountered one actually at the periphery of the disc, and measuring  $0.056 \times 0.040$  mm. in diameter.

*Vitellocytes.*—The vitellocytes in this disc, both peripheral and sub-marginal, are numerous, large, and active-looking. The peripheral vitellocytes may extend as far out as 0.14 mm. from the margin of the disc, but are mostly concentrated near the latter, lying in close contact with the egg-membrane. They possess one, two, or three nuclei, or may be multinucleate, one such attaining a diameter of  $0.075 \times 0.024$  mm. Four are in mitosis. The sub-marginal vitellocytes lie mostly in close contact with the yolk-membrane below the periphery of the disc. One is multinucleate, another binucleate, one of the nuclei being very large ( $0.024 \times 0.015$  mm. in diameter). Three appear to be in the prophase of division, and one in the anaphase.

*Platypus B and BB. Twin-eggs. (Pl. VIII, figs. 47–49.)*

These eggs were collected by J. John at the Burnett River, Queensland, so long ago as 20. viii. 01. Their state of preservation is excellent. The diameter of both eggs is given in our original notes as 6.5 mm. after fixation.

(Diameter of ovum B, 4.30 mm., and of ovum BB, 4.20 mm. Diameter of disc B,  $0.41 \times 0.368$  mm. Thickness, 0.084 mm. Diameter of disc BB,  $0.32 \times 0.42$  mm. Thickness, 0.072 mm. Shell, 0.0045 mm. in thickness. Fixation, PNO.)

The twin-discs here described are of interest as being the only examples of late blastodiscs of *Ornithorhynchus* in our collection. Both discs are at precisely the same stage of development, though as the measurements show, disc BB is slightly smaller than B, both in surface-area and in thickness. They are very similar to VVH 17, but are distinctly smaller than that stage in all their dimensions, including cell-size. Both discs appear plano-convex in section, and attain a thickness of four cells in their central region. The surface-cells, oval or rounded, or occasionally flattened, do not form a very regular superficial layer. They are less vacuolated and less rich in yolk than the deep cells. The latter are compactly arranged, and many of them are vacuolated peripherally and rich in fine yolk-spheres.

In disc B the average diameter of 24 disc-cells measured is  $0.038 \times 0.023$  mm., and of 12 nuclei  $0.011 \times 0.066$  mm. In disc BB the corresponding measurements are  $0.035 \times 0.019$  mm. and  $0.010 \times 0.050$  mm. As can be seen from the figures, the disc in its central region is sharply marked off from the yolk-bed, but in the peripheral region in both discs there are present small areas where the deep cells are still open to the yolk. In disc B the great majority of the actual peripheral cells are still in partial or complete continuity with the yolk (Pl. VIII, fig. 47, *pdc.*), whereas in BB a much larger proportion of them have become delimited (Pl. VIII, fig. 49, *pdc.*).

Yolk-balls occur, but are not very numerous.

*Vitellocytes.*—These cells are fairly numerous in both discs (Pl. VIII, figs. 48 & 49, *pv.*). In BB we have counted some 35, situated close to the disc-periphery, of which five are multinucleate and four binucleate. Two only are sub-marginal. In B there appear to be no sub-marginals, though occasionally a vitellocyte may underlie the yolk-membrane before it reaches the egg-membrane below the zona-albumen layer. The vitellocytes tend to be small, but are sometimes elongated, one binucleate cell in B measuring  $0.080$  mm. in length  $\times 0.012$  mm. in thickness. So far as we have observed, they are always situated superficially (Pl. VIII, fig. 49), close below the egg-membrane.

No sub-disc cells were observed.

*Yolk-bed.*—The yolk-bed is very similar in the two eggs, and presents a highly characteristic appearance, well seen in Pl. VIII, fig. 48 from egg BB.

Below the central region of the disc the bed consists of an area remarkably uniform in character, and containing very fine yolk-spheres only, compactly arranged. In the yolk-bed of *Echidna*, this same area is usually much vacuolated. In BB (Pl. VIII, fig. 48) it has a width of about 0.092 mm., and a depth down to the coarsely vacuolated area seen in the figure, of about 0.16 mm. Below the peripheral region of the disc, the central area merges into a narrow zone containing slightly larger spheres, and this similarly passes over without limit into the distinct marginal zone encircling the disc, which contains still larger spheres, and possesses a width in egg BB of 0.08–0.10 mm.

Pl. VIII, fig. 48 also shows very clearly the latebral neck (*yn.*) passing up to join the yolk-bed. In its lower part it appears as a thin axial cord containing



fine yolk-granules. In its upper part it gradually expands, develops coarse vacuoles and terminates in a conspicuous clear vacuolated area underlying the central part of the yolk-bed, and measuring about  $0.080 \times 0.072$  mm. in diameter. The coarse vacuoles originally occupying its central part have apparently broken down, leaving a large irregular space bordered by a few persisting vacuoles. We have observed a similar vacuolated area in this position in other *Platypus* eggs, though it is not invariably present. In egg B, a distinct more finely vacuolated tract, about  $0.064$  mm. in width, extends up from it towards the disc, but is only faintly indicated in egg BB, and is not present in the section figured.

#### *Appendix to Group II.*

The following three discs (VVH 4, *Ech.* XVII, and VVH 30) are somewhat atypical, and need only brief description.

##### VVH 4. (Pl. VIII, figs. 50 & 51.)

(Diameter of egg,  $4.2$  mm. (fresh),  $5.56$  mm. (after fixation), and of ovum,  $4.4 \times 4.3$  mm. Diameter of disc,  $0.52 \times 0.56$  mm. Thickness,  $0.176$  mm. Fixation, FBA.)

This disc, of greater diameter than that of VVH 36, shows no very definite advance on that, and like the succeeding disc (*Ech.* XVII) is somewhat atypical in that the superficial cells fail to form a continuous surface-layer. The disc-cells are larger, attaining, indeed, the maximum size met with in the Group; the average diameter of 24 cells being  $0.057 \times 0.046$  mm., and of 12 nuclei  $0.012 \times 0.011$  mm., and they are richer in yolk than those of VVH 36, the peripheral cells in particular being rich in medium sized as well as small spheres (Pl. VIII, fig. 51).

In the surface view (Pl. VIII, fig. 50), there are present about 70 superficially situated cells. From the figure it will be seen that the peripheral contour of the disc is very irregular, and that the disc consists of a central group of cells, varying somewhat in size and evidently disposed at varying levels, and an incomplete and quite irregular peripheral ring of blastomeres, larger on the whole than the central. Outside the periphery of the disc, in the ill-defined marginal zone, are a few light areas marking the position of peripheral vitellocytes, but in this disc there is no appearance of any transitory cleavage process in connection with them.

Examination of the sections reveals that the superficial cells (Pl. VIII, fig. 51) are arranged quite irregularly; some lie in contact with the zona-albumen layer, others fail to reach it, so that gaps are left between the cells and between them and the latter.

Centrally the disc attains a maximum thickness of four cells and thins out to a single cell at its periphery. The disc-cells are large, oval, or rounded in outline, and their cytoplasm is richly and finely granular. Some of the central cells contain little or no yolk, but the majority show peripheral areas of vacuolation, crowded with fine yolk-spheres.

The peripheral portion of the disc is formed of larger cells (measuring up to  $0.084 \times 0.060$  mm. in diameter) containing in addition to small, numbers of much coarser spheres (Pl. VIII, fig. 51).

Over an extent of about 0.28 mm., in the central region of the disc, the cells, both central and peripheral, are separated from the yolk-bed by a distinct, continuous yolk-membrane (Pl. VIII, fig. 51). Outside that area the yolk-membrane continues to be distinct, but many of the large peripheral cells are here open to the yolk.

It is deserving of mention that at the periphery of the disc in one section there is present a minute, oval body,  $0.018 \times 0.014$  mm. in diameter, composed of finely granular, vacuolated cytoplasm, enclosed by a definite membrane and containing one large basophil granule, surrounded by several minute ones. This curious structure presents an extraordinary resemblance to a polar body.

*Vitellocytes*.—These cells are not very numerous in this disc, but such as occur are large, with plasma-rich cell bodies and active-looking nuclei. They measure up to  $0.054 \times 0.030$  mm. in diameter, nucleus  $0.015 \times 0.012$  mm., and exceptionally may be still larger, one situated 0.012 mm. from the disc-margin reaching a diameter of  $0.060 \times 0.033$  mm., nucleus  $0.012 \times 0.010$  mm. The majority of them lie adjacent to the disc-margin, though a few lie below the yolk-membrane, where it extends up beyond the actual margin of the disc. Only one or two actually underlie peripheral disc-cells.

One peripheral vitellocyte of large size (diameter  $0.060 \times 0.030$  mm.) shows an obliquely disposed mitotic figure in the metaphase.

*Echidna* XVII (11.8.31). (Pl. IX. figs. 52 & 53.)

(Diameter of egg, 3.8 mm. Diameter of disc,  $0.50 \times 0.50$  mm. Thickness, 0.096 mm. Fixation, PNO.)

This is a curious disc, even more atypical than VVH 4, and recalling it in the absence of a definite superficial layer and the irregular, uneven character of its surface. On one side in the central sections (left in Pl. IX, fig. 52), the peripheral cells are separated by a gap from the rest of the disc.

The disc is thin, being not more than three cells thick centrally, and is sharply marked off from the yolk-bed except at its periphery, where many of the actual peripheral cells are still open to the yolk (Pl. IX, fig. 52, *pd.*).

The disc-cells, oval or rounded in outline, are large, the average diameter of 12 being  $0.052 \times 0.036$  mm., and that of their nuclei  $0.013 \times 0.010$  mm. The cytoplasm is finely granular, and in the central cells there is usually present a richly vacuolated area on one side, containing numerous fine yolk-granules. The peripheral cells are rich in much coarser spheres which are usually disposed in the lower half of the cell (Pl. IX, fig. 52, *pd.*). They are larger on the average than the central, their range in diameter being from  $0.054 \times 0.042$  mm. to as much as  $0.075 \times 0.050$  mm. The latter is a cell in the telophase, and is still open to the yolk (Pl. IX, fig. 52, *pd.*, left). We have observed another peripheral cell in a like condition, and a number of central disc-cells also in process of division.

Small yolk-balls are present between the disc-cells, and numbers of them are in process of being budded-off from the surface of the yolk-bed.

*Vitellocytes*.—These are fairly numerous and quite well developed. Most of them lie below the egg-membrane just outside the disc-margin, though a few lie below the peripheral portion of the yolk-membrane, before it reaches the zona-albumen layer and the egg-membrane. There are no sub-marginal vitellocytes



in this disc. Three vitellocytes have been observed in the prophase of division. One of them is shown in Pl. IX, fig. 53 (*pv.*); it measures  $0.054 \times 0.013$  mm. in diameter, and is situated 0.07 mm. beyond the disc-margin. Another possesses two minute nuclei in process of being reconstituted after division, and one is binucleate.

VVH 30. (Pl. IX, fig. 54.)

(Diameter of egg 4.5 mm. (fresh),  $5.5 \times 5.0$  mm. (after fixation). Diameter of disc,  $0.370 \times 0.376$  mm. Thickness, 0.10 mm. Fixation, Bouin-Hollande.)

In surface-extent this disc is the smallest in the Group, and it is also one of the thinnest, being of practically the same thickness as that of *Ech.* XVII. Moreover, it projects more from its concavity in the yolk-bed than do the other discs in the Group, possibly owing to a greater contraction of the surrounding marginal yolk, induced by the fixative.

In section (Pl. IX, fig. 54), the disc presents a very compact "button-like" appearance, its cells lying in close apposition. Centrally it is four cells thick, whilst at its periphery, it is mostly one, sometimes two cells thick. It is clearly delimited from the yolk-bed right out to its periphery, except in two isolated areas shortly within the latter, where it is still open to the yolk.

The superficial layer is well marked, though not very regular. Its cells are mostly poor in yolk and not greatly vacuolated. The deep disc-cells in the central region tend to be more vacuolated, but are also poor in yolk, though some of the cells adjoining the yolk-membrane are densely crowded with coarse and fine spheres. In the peripheral region yolk-laden cells, both superficial and deep, are more frequent, though only a few of the actual peripheral cells contain yolk-spheres.

The average diameter of 12 disc-cells measured is  $0.040 \times 0.025$  mm.

*Vitellocytes.*—These cells are not very numerous and are mainly located below the egg-membrane close to the disc-margin. About eight of them are sub-marginal. Two of the latter and one peripheral are binucleate, whilst two sub-marginals are very large, one measuring 0.081 mm. in length  $\times$  0.021 mm. in thickness, the other  $0.060 \times 0.018$  mm. Each of them possesses four nuclei.

### GROUP III.

This group comprises eight stages of *Echidna* (VVH 35, 27, 14, 9, *Ech.* 30 (11.7.30), VVH 47, 45 and 6 in order of age), which form a very complete series ranging from the earliest stage VVH 35 with a *blastodisc*, 6–7 cells thick, and measuring in diameter  $0.56 \times 0.56$  mm., and in thickness 0.136 mm., to the most advanced stage VVH 6 with a *blastoderm*, about two cells thick, a diameter of  $1.36 \times 1.38$  mm. and a thickness of 0.032 mm. The very striking advance thus indicated, from blastodisc to blastoderm, marks a developmental phase of the greatest interest and importance, involving as it does the formation of the marginal syncytial ring or germ-ring and the correlated growth in surface-extent of the blastodisc and its gradual transformation into a relatively thin blastodermic membrane, capable of growing round to enclose the yolk-mass of the egg.

Furthermore, study of the later stages included in the group has enabled us to establish the significant fact that the constituent cells of these early blastoderms

can be grouped into two categories, with distinctive cytological characters and endowed with predetermined potencies, as subsequent stages show, for they can be followed through the latter until they finally become segregated to form the two primary germ-layers. These two types of cell may accordingly be designated as prospective ectodermal cells and primitive endoderm cells (endoderm mother-cells) respectively.

VVH 35. (Pl. IX, figs. 55–57; Pl. X, figs. 58–61.)

(Diameter of egg, 4.5 mm. (fresh), 5.7 mm. (after fixation), and of ovum, 4.4 mm. Diameter of disc,  $0.56 \times 0.56$  mm. Thickness, 0.136 mm. Fixation, FBA.)

This disc, the earliest in the Group III series, is of the greatest importance, since in it the germ-ring makes its first appearance, although it is still incomplete. Round a little more than half the perimeter of the disc it is present as a continuous structure, over the remainder it is still in process of formation.

In its general structure the disc recalls that of VVH 41. It is, however, of slightly greater diameter, and the surface view (Pl. IX, fig. 55) shows that its periphery is now much more regular and much better defined than in that stage, though there are still present a few projecting cells and two small protuberant cell-groups. Moreover, the number of surface-cells is considerably greater than in VVH 41, being approximately 350 as compared with 220 in the latter. It may be noted also that the largest cells occur round the periphery, notably on the left side in the figure.

The disc (Pl. IX, figs. 56 & 57) is 6–7 cells deep in its central region, its maximum thickness being 0.136 mm. as compared with 0.128 mm. in VVH 41. At the periphery it is mostly one cell thick over a width varying from 1–3 cells, but in a few places it is two cells in thickness. Though the germ-ring has in larger part been established, there is no clear evidence that the disc has as yet commenced to spread.

The disc-cells are somewhat smaller than in VVH 41, the average diameter of 24 cells being  $0.027 \times 0.023$  mm. and of 24 nuclei  $0.009 \times 0.0085$  mm., and as in that disc they are characteristically rounded or oval in outline, the deep cells being separated by well-marked intercellular spaces in which yolk-balls occur.

The surface-cells form a fairly definite superficial layer, and over the central region are mostly yolk-free and little vacuolated, and the same holds true for the underlying deep cells, except that adjoining the yolk-membrane, large yolk-laden cells are of frequent occurrence. In the peripheral region also, vacuolated yolk-laden cells are numerous, and often reach a large size (up to  $0.060 \times 0.045$  mm. in diameter, nucleus  $0.012 \times 0.010$  mm.). Some of them are clear and crowded with minute spheres, varying slightly in diameter, but others contain medium coarse as well as fine spheres. A few of the deep peripheral cells are still open to the yolk-bed, otherwise the disc is clearly delimited. The great majority of the actual peripheral cells appear to be delimited. Many of them are large (up to  $0.051 \times 0.039$  mm. in diameter) and rich in yolk, others, smaller, are yolk-free.

In view of the connections which are eventually established between the peripheral disc-cells and the germ-ring, it is perhaps worthy of mention that a deep disc-cell indents the surface of the large multinucleate sub-disc vitellocyte situated below the central region of the disc in Pl. IX, fig. 57 (*smv.*), its limiting membrane



being closely soldered to the surface of the vitellocyte or rather to the yolk-membrane covering it.

Part of the under-surface of a second deep cell is also closely attached to the same cell, and we have observed another small, deep disc-cell attached to the surface of a sub-marginal vitellocyte by three very slender processes. It should be mentioned, however, that it is quite common to find deep disc-cells lying in close apposition with the yolk-membrane, in the complete absence of underlying cells.

*Vitellocytes and Germ-ring.*—As stated above, the germ-ring is now established as a continuous formation round rather more than half the perimeter of the disc, whilst over the remainder the vitellocytes there present, both peripheral and sub-marginal, are large, binucleate or multinucleate, and are in process of becoming linked together by cytoplasmic connections, mostly still thin, preparatory to their complete fusion to form the remainder of the ring.

Seen in transverse section (Pl. X, fig. 60), the germ-ring appears as a relatively thin layer of cytoplasm, somewhat spindle-shaped in form, which extends outwards from the margin of the disc for a distance (in the section figured) of 0.23 mm. It attains its greatest thickness (0.018 mm.) about 0.075 mm. from the disc-margin, and in this thickened region a large oval nucleus ( $0.021 \times 0.010$  mm. in diameter) is situated. The nuclei usually occur singly, though sometimes two occur together. They are mostly large and stain fairly deeply. On either side of the thickened region, the ring becomes much thinner, the reduction in thickness being most marked on its outer side.

The germ-ring varies in width from about 0.10 to 0.23 mm., and it also varies considerably in thickness over its extent, as just indicated, and from section to section, its thickness ranging from about 0.006 mm. in its peripheral region to 0.018 mm. in its thickened region. It is composed of finely granular cytoplasm, minutely vacuolated and staining rather deeply in its inner half or thereabouts, and more coarsely vacuolated and less deeply staining in its outer half. Imbedded in the cytoplasm just above its under-surface are numbers of small yolk-spheres as well as minute yolk-granules. Its upper surface presents a smooth, even contour, and on careful examination is seen to be invested by a thin membrane, the egg-membrane. Its under-surface, on the other hand, is quite irregular, and lacks a definite boundary, since its cytoplasm, like that of the vitellocytes from which it has been formed, is produced into delicate prolongations which pass down between the yolk-spheres into continuity with the fine cytoplasmic reticulum pervading the more superficial portion of the marginal zone. In the meshes of the network so formed, the yolk-spheres immediately underlying the germ-wall lie enclosed, whilst numbers of minute yolk-granules are present in the mentioned prolongations as well as in the strands of the reticulum itself.

At its inner margin the germ-ring either abuts directly on the outer ends of the peripheral disc-cells or it may extend inwards below them for a very short distance as a thin vacuolated prolongation (as seen in Pl. X, fig. 60), in which case the whole or part of the under-surface of the peripheral cell usually lies in more or less intimate apposition with its surface. Only in one instance have we observed a peripheral cell connected with the surface of the germ-ring by a very short process arising from its outer end. In this case the peripheral cell is separated from the

inward continuation of the germ-ring by a minute cleft-like space, which is closed on its outer side by the mentioned process.

The outer limit of the germ-ring is difficult to determine precisely, since it becomes very attenuated, and merges into the very thin, ill-defined cytoplasmic layer (about 0.003 mm. or less in thickness) representing the remains of the peripheral cytoplasmic zone of the oocyte (*v.* Part IV, p. 466) which underlies the egg-membrane, and which extends outwards for only a very short distance beyond what we take to be the peripheral limit of the ring. It would probably pass unnoticed but for the presence in it of minute yolk-granules and small spheres. Evidently, where the germ-ring has been established, only a peripheral fragment of this layer remains intact, by far the greater part of it having been incorporated in the vitellocytes during the formation of that structure. On the opposite side of the disc, in the gap where vitellocytes are absent (referred to below), the layer in question is seen in its full extent and is much more distinct, appearing as an attenuated layer of cytoplasm, hardly staining but distinctly vacuolated in places, and containing numbers of small yolk-spheres and minute yolk-granules. It has a maximum width of about 0.30 mm., measured from the periphery of the disc. The vitellocytes are in continuity with this layer at their peripheries, and must have fused with it over their areas of contact with the egg-membrane, so that it must be regarded as contributing in some small measure to the formation of the germ-ring.

The germ-ring has a width of 0.11 mm. immediately in front of the disc, and of 0.13 mm. just behind it, as measured in the serial sections, and in both regions is, of course, cut tangentially. Its appearance behind the disc is illustrated in Pl. X, fig. 61.

Turning now to the region of the disc-periphery where the germ-ring is in process of completion, we find the ring is present on this side in the first six sections through the disc. Then it passes into a large multi-nucleate peripheral vitellocyte, measuring  $0.081 \times 0.060$  mm. in diameter  $\times 0.025$  mm. in thickness, and possessing vacuolated cytoplasm and 10–11 nuclei. Four sections farther on in the series, when it has become much reduced in size, this cell (Pl. X, fig. 58, *pv.*) becomes connected by a thin layer of cytoplasm underlying the egg-membrane with the binucleate sub-marginal vitellocyte (*smv.*) seen in the figure. This latter cell measures  $0.036 \times 0.030$  mm. in diameter and 0.021 mm. in thickness, and lies directly below a peripheral disc-cell which is in contact with it by the outer and inner edges of its lower surface. A little farther on in the series, two peripheral vitellocytes appear, which are connected by a thin layer of cytoplasm. The one nearer the disc-margin is the larger ( $0.07 \times 0.06$  mm. in diameter  $\times 0.018$  mm. in thickness), and possesses eight nuclei; the other is binucleate, and has a diameter of about  $0.06 \times 0.04$  mm. and a thickness of 0.018 mm. Then an isolated sub-marginal vitellocyte follows ( $0.051 \times 0.04$  mm. in diameter  $\times 0.027$  mm. in thickness) in which no nuclei were observed. Next in the series appear the two vitellocytes seen in Pl. X, fig. 59; one (*pv.*), peripheral, ( $0.072 \times 0.06$  mm. in diameter and 0.036 mm. in thickness) with three nuclei, the other (*smv.*), partly sub-marginal, ( $0.090 \times 0.060$  mm. in diameter and 0.033 mm. in thickness) possessing six nuclei and a slender connection with the just mentioned peripheral vitellocyte. It is noteworthy that the peripheral disc-cell which overlies the inner portion of this sub-marginal vitellocyte seems to be in process



of acquiring connection with it. It is produced into a blunt slightly curved projection which is directed towards a slight elevation on the surface of the vitellocyte, and during life may well have been in contact with it. In addition a very slender connection between the two appears to have been established by a fine process arising from the mid-region of the under-surface of the peripheral cell (Pl. X, fig. 59).

Following on the preceding two cells an isolated peripheral vitellocyte, lying 0.12 mm. from the disc-margin, appears. It is binucleate and measures  $0.054 \times 0.040$  mm. in diameter and 0.018 mm. in thickness. Then follows a gap of 0.08 mm. where no vitellocytes occur, and this is succeeded by a large peripheral vitellocyte, situated 0.072 mm. from the disc-margin, and measuring  $0.010 \times 0.080$  mm. in diameter  $\times 0.030$  mm. in thickness. Its nucleus is quite minute (about  $0.007 \times 0.0015$  mm. in diameter). This cell establishes a slender connection with a peripheral vitellocyte which appears a few sections farther on in the series, and lies nearer the disc-margin. It is trinucleate and measures  $0.075 \times 0.050$  mm. in diameter  $\times 0.024$  mm. in thickness. Another smaller vitellocyte ( $0.057 \times 0.030$  mm. in diameter  $\times 0.027$  mm. in thickness) next appears still nearer the disc-margin and partly underlying it. It is apparently devoid of a nucleus and is possibly connected with the preceding cell.

Finally, practically on a level with the hinder margin of the disc (in the series), three vitellocytes appear. One (Pl. X, fig. 61, *pv.* 1) is partly sub-marginal and is trinucleate. It measures  $0.048 \times 0.060$  mm. in diameter  $\times 0.030$  mm. in thickness, and becomes continuous behind the disc with the germ-ring (*gr.*) of the opposite side. It is also connected with a second peripheral vitellocyte (*pv.* 2) which lies adjacent to it, is binucleate and measures  $0.054 \times 0.040$  mm. in diameter  $\times 0.018$  mm. in thickness. The third cell (Pl. X, fig. 61, *pv.* 3) is large, measuring  $0.072 \times 0.070$  mm. in diameter  $\times 0.021$  mm. in thickness. It is devoid of a nucleus, and is apparently still isolated.

Altogether there are 14 vitellocytes on this side of the disc where the germ-ring is in process of formation. Of these, five may be regarded as sub-marginal or partly so, and nine are peripheral. In three of them no nuclei were observed, the remaining eleven possess between them the remarkably large total of forty nuclei. Another noteworthy feature of these vitellocytes is the large average size they attain. Possibly some of them may have been formed by the fusion of originally separate cells. From the foregoing, it is clear that the germ-ring is a syncytial formation which owes its origin to the concentration, enlargement, and fusion of peripheral and sub-marginal vitellocytes around and immediately below the periphery of the blastodisc.

*Yolk-bed cells.*—Four such cells are present. They all appear to be of the nature of inwandered sub-marginal vitellocytes. The largest of the four is seen in Pl. IX, fig. 57 (*smv.*), underlying the central region of the disc, its upper surface being closely attached to or fused with the yolk-membrane. It measures  $0.072 \times 0.050$  mm. in diameter  $\times 0.040$  mm. in thickness, and possesses five nuclei, varying in size, the largest  $0.021 \times 0.016$  mm. in diameter. Two others are situated about 0.18 mm. within the disc-margin, one on each side of the same section. Both are multinucleate. The fourth, situated below the peripheral region of the disc is small and uninucleate (Pl. IX, fig. 57, *smv.*, on the left).

VVH 27. (Pl. X, fig. 62; Pl. XI, fig. 63.)

(Diameter of egg, 5.0 mm. (fresh), 5.67 mm. (after fixation), and of ovum,  $4.7 \times 4.4$  mm. Diameter of disc,  $0.650 \times 0.688$  mm. Thickness, 0.104 mm. Fixation, FBA.)

This disc has already commenced to increase in surface-extent, as is indicated by its increase in diameter and its decrease in thickness, as compared with the preceding disc (VVH 35), and also by the thinness of its marginal region which has become one-cell thick over a width in places of 4–5 cells.

The surface view of the disc (Pl. X, fig. 62) shows that it possesses an oval outline, and that its periphery is much more regular and even than that of VVH 35. In its central region the cells are small and of fairly uniform size, in its peripheral region they are larger, noticeably so round the upper, and adjoining right and left margins in the figure.

The surface view (Pl. X, fig. 62) conveys an excellent idea of the general appearance of the disc, as seen under the binocular stereoscopic microscope and in photographic enlargements, but the detailed representation of the surface-cells, now much reduced in size, must necessarily be somewhat schematic, so that the number visible in the figure (about 370) can only be regarded as an extremely rough approximation to the number actually present. The same remark applies to the other surface views included in the series.

Seen in section, the disc (Pl. XI, fig. 63) now presents a characteristically loose, spread-out appearance, in sharp contrast with the compact character of the disc in VVH 35. In its central region it is now about five cells in depth, and correspondingly it shows a definite decrease in thickness to 0.104 mm. as compared with 0.136 mm. in VVH 35, due partly to the decrease in the number of superimposed cells, partly to their smaller size, the average diameter of 35 cells being  $0.023 \times 0.018$  mm., and that of their nuclei  $0.0078 \times 0.0075$  mm.

The characteristic appearance of the disc in section is due to the loose open arrangement of the deep cells in its central region. The cells are mostly rounded in form, and large intercellular spaces occur between them, whilst large spaces are also present in the peripheral region. In these spaces yolk-balls are present in fair numbers. They are mostly small (about 0.006 mm. in diameter), though some of them are quite large (up to  $0.036 \times 0.030$  mm.). Their cytoplasmic basis is crowded with small spheres of varying size.

The superficial layer of the disc is continuous, with only an occasional gap, and is composed over the central region of rounded and ovalish cells, the latter frequently connected by their attenuated ends. They are sometimes slightly vacuolated, and may contain sparse fine yolk-spheres, whilst sporadic yolk-laden cells are also met with. Some of the deep cells are free from yolk, but mostly they are vacuolated, and contain yolk-spheres in greater or less abundance. They may reach a large size (up to  $0.039 \times 0.033$  mm. in diameter, nucleus  $0.013 \times 0.012$  mm.), and may be densely laden with medium large and fine spheres, or with the latter alone. Many of the vacuolated deep cells contain numbers of minute yolk-spheres which stain a dull red with eosin, and are evidently in process of digestion.

In the peripheral region, large yolk-laden cells are abundantly present, both in the deep and superficial layers. In this region the disc tends to thin out to a thickness of one cell, over a width in places of up to four or five cells, and here



the peripheral cells are frequently yolk-laden and of large size, one such cell attaining a diameter of  $0.075 \times 0.042$  mm., and possessing two large nuclei. The actual peripheral cells are mostly large and yolk-laden.

The disc is clearly marked off from the yolk-bed (Pl. XI, fig. 63), though there are one or two places where the yolk-membrane appears to be interrupted.

*Germ-ring.*—The germ-ring is now established all round the disc, but it is narrow and thin. Its width varies from about 0.13 to 0.18 mm. (exceptionally 0.24 mm.), whilst its thickness ranges from about 0.012 to 0.018 mm., though in one or two sections it reaches 0.024 mm. It is traceable for about 0.14 mm. in front of the disc and about 0.15 mm. behind it.

It is still irregularly fusiform in section, reaching its greatest thickness at a variable distance (ranging from 0.03 to 0.10 mm.) from the margin of the disc, and thinning out on either side, and most markedly on its outer side, where it becomes very attenuated towards its periphery. On its inner side, over parts of its extent, especially on one side of the disc, it looks at first sight as if it terminated before reaching the peripheral disc-cells, but more careful examination shows that it really continues on (over a width varying from 0.015 to 0.045 mm.) as a very delicate cytoplasmic reticulum enclosing small yolk-spheres.

At its inner margin the germ-ring may continue inwards for a very short distance below the disc-margin. There it comes into close apposition with the outer ends of the peripheral disc-cells and frequently also with the under-surfaces of the same, or it may make contact only with the latter, in whole or in part, the two surfaces of contact having the appearance of being intimately adherent the one to the other. Occasionally the under-surface of the peripheral cell fails to make complete contact with the germ-ring, a minute cleft partially separating the two. In one case, the cleft is large and curved, completely separating the two surfaces, and the peripheral cell is attached to the germ-ring only by its bluntly pointed outer end.

The germ-ring is composed of rather coarsely granular, finely vacuolated cytoplasm, which encloses especially towards its underside numbers of fine yolk-granules and small yolk-spheres. Its nuclei usually occur singly in the sections, more rarely in pairs, and still more rarely in nests of four or five. They vary in diameter up to a maximum of  $0.024 \times 0.009$  mm.

*Yolk-bed cells.*—There are some six of these cells below the disc. One, attached to the yolk-membrane, possesses four nuclei, and is exceptional in enclosing in its cytoplasm a medium-sized yolk-sphere as well as several smaller spheres. A second is also attached to the yolk-membrane, and is devoid of a nucleus. The remaining four are situated shortly below the disc (one of them 0.032 mm. below the yolk-membrane); one possesses five nuclei, one has three, and two with shrunken cell-bodies are each binucleate.

VVH 14. (Pl. X, fig. 64; Pl. XI, figs. 65 & 66.)

(Diameter of egg,  $6.0 \times 4.5$  mm. (fresh),  $7.00 \times 4.34$  mm. (after fixation), and of ovum,  $4.7 \times 4.3$  mm. [Egg ovoidal in form, with one end more pointed (v. Part IV, Pl. XXI, fig. 116)]. Diameter of disc,  $0.68 \times 0.69$  mm. Thickness, 0.096 mm. Fixation, FBA.)

This is a fine disc (Pl. X, fig. 64) and shows continued progress. It is practically circular in outline, and its periphery is definite and almost quite regular. The surface-cells, numbering approximately 500, are now more uniform in size, though in the peripheral region, on the right side of the disc (in the figure), the cells tend to be slightly larger than elsewhere. The light marginal zone around the disc is very distinct, and varies from 0.32 to 0.48 mm. in width.

The disc is only a very little larger and just a little thinner than that of VVH 27, and generally resembles it, but its cells are more loosely arranged, and in the peripheral region are much less rich in yolk-spheres, whilst the germ-ring has attained a more massive form, and altogether is better developed than in that disc.

The disc centrally may attain a thickness of five cells, but owing to the presence of large irregular spaces between the deep cells it is only occasionally that one finds five cells directly superimposed. Such spaces, well marked in the central region, are even more prominent in the peripheral region (Pl. XI, fig. 65).

The disc-cells are a little larger than those of VVH 27, the average diameter of twenty cells measured being  $0.025 \times 0.019$  mm., and of their nuclei  $0.009 \times 0.008$  mm.

The surface-cells over the central region form a somewhat irregular superficial layer; the cells are rounded or oval, sometimes pointed at their ends, and mostly devoid of yolk and not greatly vacuolated. The deep central cells are mostly rounded and loosely arranged. They are often vacuolated, and are much less yolk-rich than those of VVH 27. In the peripheral region, which tends to be thin with sparse deep cells, the superficial cells are often vacuolated, and may contain numerous fine or a few small or medium-sized spheres, and the same holds true for the deep cells (Pl. XI, fig. 66). The actual margin of the disc may be one cell thick or, as is frequently the case, two cells thick, and in this case the deep cell is usually large and rich in yolk-spheres. Many of the disc-cells are in mitosis, the dividing cells being about equally distributed amongst the superficial and the deep.

Numerous yolk-balls are present in the intercellular spaces throughout the disc. They are mostly small, but some of them are quite large (up to  $0.04 \times 0.026$  mm. in diameter).

Except for one or two deep cells at the periphery, the disc is clearly delimited from the yolk-bed.

*Germ-ring.*—This is well developed all round the disc (Pl. XI, figs. 65 & 66, *gr.*). It is thicker and much more massive than that of VVH 27, and much more concentrated close to the disc-margin. It varies somewhat in width and in thickness over its extent, and in the sections is thicker on one side of the disc than on the other; *e. g.*, in Pl. XI, fig. 65, it measures on the left  $0.168$  mm. in width  $\times 0.045$  mm. in thickness, and on the right  $0.12 \times 0.024$  mm. Its maximum width is about  $0.184$  mm., and its maximum thickness about  $0.054$  mm.

The ring (Pl. XI, fig. 66) attains its greatest thickness adjacent to the disc-margin, and rapidly becomes reduced peripherally to a relatively thin layer which finally merges into the peripheral cytoplasmic layer. On its inner side the dense cytoplasm forming its main bulk passes rather abruptly below the peripheral disc-cells into continuity with the cytoplasmic reticulum of the yolk-bed, lying immediately below the yolk-membrane. This reticulum is exceptionally distinct



in this disc. In its strands occur fine yolk-granules, whilst small yolk-spheres are included in its meshes.

The main thickness of the germ-ring is formed of a layer of finely granular cytoplasm, rather dense and deeply staining, and usually only slightly vacuolated in its inner thicker part, but richly vacuolated in its thinner peripheral region. Below, this dense cytoplasm merges into a narrow much lighter staining zone of reticular cytoplasm, enclosing fine yolk-granules and small yolk-spheres of varying size. Its nuclei mainly lie in its thicker part; they are numerous (from one to six occurring in a single section), and are often large (up to  $0.027 \times 0.016$  mm.), though numbers of small nuclei (from  $0.006 \times 0.005$  mm. in diameter upwards) are present as well. We have failed to find any evidence of mitotic division, but there is evidence of the occurrence of direct nuclear division by a process of budding, as is indicated also by the occurrence of small nuclei alongside the large.

The relations of the peripheral disc-cells to the germ-ring are now of a more intimate character than in the preceding stage. The ring, on reaching the disc-margin, may slope quite gradually downwards and inwards below the peripheral cell (Pl. XI, fig. 66), a slight ridge often marking the beginning of the slope, or it may be depressed so as to form a shallow groove bounded on its outer side by an almost vertical face, in which the lower half of the peripheral cell or the peripheral deep cell (where the margin is two cells thick) is lodged. In the former case the limiting membrane of the under-surface of the peripheral cell, in whole or in part, may be intimately adherent to or fused with the surface of the ring (formed by the egg-membrane), or, more rarely, the outer end of the peripheral cell may give off a minute projection which connects with that surface or with the ridge above mentioned. In the latter case, the outer and under-surfaces of the cell occupying the depression may be intimately adherent to the surface of the ring in whole or in part. When the disc-margin is two cells thick, the deep cell may exclude the superficial from making contact with the germ-ring, or both may be connected therewith, the latter by means of a slender process, passing round the outer end of the deep cell.

It remains to be mentioned that below the peripheral region of the disc two sub-marginal vitellocytes are still recognizable, though they are in continuity with the germ-wall. One of the two is large, measuring  $0.051 \times 0.070$  mm. in diameter  $\times 0.027$  mm. in thickness, and is multinucleate (possessing eight or more nuclei). It is adherent to the yolk-membrane, and is in continuity with the germ-ring by a thin sub-marginal extension of the same which runs inwards from the level of the disc-margin for a distance of 0.07 mm. The second sub-marginal underlies three of the peripheral disc-cells. It measures  $0.066 \times 0.060$  mm.  $\times 0.021$  mm. in thickness, possesses four nuclei, and is also in direct continuity with the germ-ring. In this connection it may also be mentioned that at two places on opposite sides of the disc the ring is prolonged inwards below the latter for a greater distance than is normal. In one case the prolongation extends inwards for a distance of 0.090 mm. from the disc-margin, and possesses a single nucleus. The other is more extensive. It runs inwards as a tapering process for a distance of 0.15 mm. from the margin, has a thickness of 0.015 mm. near the middle of its extent, and a width in the sections of 0.060 mm. It possesses a group of about six nuclei, situated below and just laterally to the peripheral disc-cell. These apparent

inward extensions are doubtless also formed by sub-marginal vitellocytes.

*Yolk-bed cells.*—Two only appear to be present. One is large (Pl. XI, fig. 66, *yc.*), measuring about  $0.045 \times 0.024$  mm. in diameter  $\times 0.07$  mm. in thickness, and is multinucleate, the nuclei varying in diameter up to  $0.024 \times 0.015$  mm. Both the cytoplasm and the nuclei are strongly eosinophil. This cell lies shortly below the yolk-membrane, in the peripheral region, but it gives off a prolongation which extends up to become attached to that membrane, being coarsely vacuolated below its attachment. It is probably to be regarded as a sub-marginal vitellocyte. The other cell is represented by a minute mass of cytoplasm, devoid of a nucleus, and closely applied to the yolk-membrane.

*Latebra and yolk-bed.*—These structures present certain unusual features to which attention may be drawn.

The normal latebral body, which is coarsely vacuolated and rich in yolk-granules, is replaced in this egg by a solid mass of small yolk-spheres (about 0.32 mm. in height  $\times 0.16$  mm. in thickness). The latebral neck passing upwards from it, in the first part of its course, is curved (quite unusual), coarsely vacuolated and crowded with pale staining eosinophil granules, in these latter respects resembling the normal latebral body. Traced upwards it becomes less vacuolated (its eosinophil granules being replaced by minute basophil yolk-spheres), and passes over above into an elongated, triangular, coarsely vacuolated area, recalling that in the egg of *Platypus* BB (Pl. VIII, fig. 48). This finally merges into the central zone or core of the yolk-bed, here composed of fine basophil spheres, with amongst them numbers of much coarser spheres, and exhibiting but slight evidence of vacuolation, quite unlike the usual condition in the egg of *Echidna*, but again recalling that of the *Platypus* egg. The cytoplasmic reticulum of the yolk-bed is exceptionally distinct immediately below the yolk-membrane.

VVH 9. (Pl. XI, figs. 67 & 68.)

(Diameter of egg \*, 4.5 mm. (fresh),  $5.25 \times 5.09$  mm. (after fixation). Diameter of disc,  $0.83 \times 0.68$  mm. Thickness, 0.072 mm. (mostly 0.064–0.068 mm.). Fixation, FBA.)

As will be seen from the surface view (Pl. XI, fig. 67), the disc is somewhat atypical in being of an oval, elongated form, its long diameter being 0.14 mm. greater than the maximum diameter of the preceding disc, and its short diameter being the same as that of the latter. In addition to being larger, it is distinctly thinner than VVH 14, its maximum thickness 0.072 mm. comparing with 0.096 mm. in the latter.

As the surface view shows, the periphery of the disc is fairly regular, except on the lower side (in the figure), where it is rather uneven, with two large out-jutting cells. These are recognizable in the sections (which cut the disc parallel to its long axis) as large yolk-laden cells, one measuring  $0.052 \times 0.034$  mm. in diameter, the other  $0.044 \times 0.032$  mm.

The disc has a maximum thickness of three cells centrally. In section (Pl. XI, fig. 68), it presents a more extended appearance than that of VVH 14, and owing to the partial flattening out of the concavity on the surface of the yolk-bed, appears more superficially situated.

\* This egg, from the right uterus, was accompanied by a small abnormal egg, 2.7 mm. in diameter (fresh).



The surface-cells form a rather loose, irregular superficial layer in which there are fairly numerous gaps. The cells are oval or rounded, only occasionally vacuolated, and possess little or no yolk, except in the peripheral region, where the cells, both superficial and deep, are often vacuolated and rich in fine as well as larger yolk-spheres. The periphery of the disc is mostly one cell thick, the majority of the cells being rich in yolk.

The deep cells in the central region are loosely arranged, large spaces occurring between them. They are often vacuolated, and the majority are yolk-free.

The average diameter of 28 disc-cells measured is  $0.027 \times 0.021$  mm., that of their nuclei  $0.008 \times 0.007$  mm. The disc-cells seem to conform to one type, though we have noted the presence of numbers of small rounded cells, with deeply staining nuclei, about 0.006 mm. in diameter.

Yolk-balls are quite numerous between the deep cells, and even occur in the gaps in the superficial layer and on the surface of the same.

*Germ-ring.*—The germ-ring (Pl. XI, fig. 68) is not nearly so well developed as in the preceding stage. As usual it varies in width and in thickness over its extent, its maximum width being about 0.18 mm., and its maximum thickness 0.018 mm. It is of more uniform thickness than in VVH 14, thinning out only towards its peripheral limit, and showing no increase adjacent to the disc-margin, with the result that its nuclei are more dispersed than in the latter. On reaching the disc-margin it slopes very slightly downwards, and terminates below the peripheral cells. The under-surfaces of the latter lie in more or less close apposition with its surface, but on the whole the relationship is less intimate than in VVH 14, since in many of the cells only part of the under-surface effects contact with it.

*Yolk-bed cells.*—No such cells have been observed in this disc, but at three places in the serial sections there is present a cell-like body in the form of a delicate eosinophil reticulum enclosing large vacuolar spaces and situated immediately below, and in close contact with the yolk-membrane. These structures are probably the degenerate remains of such cells.

The remaining four stages in this Group, viz., *Ech.* 30, VVH 47, 45 and 6, are of three-fold interest and importance.

(1) The *blastodisc* has now increased so much in surface-area and has become so reduced in thickness that it can no longer be appropriately described as such, but must be regarded as having become transformed into a *blastoderm*.

(2) As already stated, examination of these stages has enabled us to establish the highly significant fact that from now on the constituent cells of the blastoderm can be grouped into two categories with distinctive cytological characters, and as the sequel shows, with quite distinct potentialities. The cells of these two categories, irregularly intermingled with each other in the stages mentioned, can be followed through the succeeding stages until they finally become segregated into two independent layers, respectively superficial and deep, which constitute the two primary germ-layers. Accordingly we shall speak of these two types of cell as prospective ectodermal cells (pros. ect.) and primitive endoderm cells (pr. end.) respectively.

(3) In the two most advanced members of the Group, VVH 45 and 6, we see initiated the cell movements which result in the attainment by the blastoderm of the unilaminar condition characteristic of the members of Group IV. These movements constitute the initial step in the process of germ-layer formation.

*Ech.* 30 (11.7.30). (Pl. XII, figs. 69–74.)

(Diameter of egg, 4.1 mm. (fresh), 5.4 mm. (after fixation). Diameter of ovum, 3.8 × 3.7 mm. (small). Blastoderm, diameter in alcohol, 1.20 × 1.09 mm., in section, 0.96 × 1.0 mm. Thickness, 0.032 mm. (mostly 0.028–0.030 mm.). Fixation, FBA.)

This stage, our earliest blastoderm, shows a marked advance on the VVH 9 blastodisc. Its surface-area is definitely greater, but the most marked difference between the two is seen in the reduction in thickness which it has undergone, its thickness being less than half that of VVH 9 and less than one-quarter that of the earliest member of the Group, VVH 35.

In surface view (Pl. XII, fig. 69), the blastoderm is seen to be oval in outline, with a sharply defined periphery. Within the latter is a light marginal zone, broader and better defined on the left side than on the right (in the figure), which encloses a darker mottled area, slightly excentric, and with an irregular lightish patch centrally. The latter patch seems to correspond to the vacuolated central core of the yolk-bed, and the darker area to the surrounding fine-grained region of the same.

In section (Pl. XII, figs. 70 & 71), the blastoderm strikingly contrasts with the blastodisc of VVH 9, not only in respect of its greater diameter and its much reduced thickness, but especially in the fact that it is much more clearly distinguishable into a thicker central region and a thinner peripheral region (*cf.* Pl. XIII, fig. 76 of the succeeding stage, VVH 47).

The central region overlies the central core and the immediately adjoining portion of the fine-grained zone of the yolk-bed (Pl. XII, fig. 71). It is 2–3 cells in depth, and attains a maximum thickness of 0.032 mm., though its average thickness is only about 0.028 mm. Its width in the central sections is about 0.26 mm., whilst the width of the peripheral region is about 0.36–0.38 mm.

In the central region the superficial layer is continuous, but not very regular, and is composed of oval, rounded or oblong cells, almost entirely devoid of yolk-spheres and only occasionally vacuolated (Pl. XII, figs. 70 & 71). The underlying cells are irregularly arranged, one to two deep. They are mostly yolk-free, and many of them contain one or more large vacuoles.

The average diameter of 25 cells measured is 0.017 × 0.012 mm., and that of their nuclei 0.007 × 0.0064 mm. They are thus distinctly smaller than those of the preceding stage. They range in diameter from 0.021 × 0.019 mm. to 0.013 × 0.005 mm.

The peripheral region is formed by the continuation of the superficial layer of the central region, with occasional deep cells below it. The superficial cells are at first very similar to those of the central region, but traced outwards they become larger, attaining their maximum size in the marginal zone over a width of from about 0.16 to 0.20 mm., and here the majority of the cells, both superficial and deep, are rich in medium-sized and fine yolk-spheres (Pl. XII, fig. 74), though



there is considerable variation in this respect from place to place (*cf.* Pl. XII, fig. 73 with fig. 74). The periphery of the blastoderm is usually one cell, occasionally two cells thick, the cells tending to be large and rich in yolk-spheres, mostly basophil, but sometimes eosinophil (Pl. XII, figs. 73 & 74). Their under-surfaces mostly lie in close apposition with the surface of the germ-ring (Pl. XII, fig. 73), and where the latter is hollowed out to receive them, their outer surfaces as well come into intimate contact with it (Pl. XII, fig. 74). In addition, in the latter figure, a minute projection from the germ-ring is seen to overlap the outer extremity of the peripheral cell. In a few instances the peripheral cell is connected with the germ-ring only by its bluntly pointed outer end.

We have observed one instance of what we take to be a deep cell almost completely imbedded in the yolk-bed shortly within the margin of the blastoderm. The cell in question is large (measuring  $0.031 \times 0.027$  mm. in diameter), is greatly vacuolated, and contains sparse yolk-spheres, whilst its centrally situated nucleus is small ( $0.007 \times 0.006$  mm. in diameter) and degenerate-looking. Similar "buried" cells are also met with in the succeeding stage, VVH 47.

*Constitution of the Blastoderm.*—After we had established the fact of the existence of two types of cell—prospective ectodermal cells and primitive endoderm cells—in the blastoderm of VVH 47 and succeeding stages, we re-examined the present blastoderm, and are satisfied that the same two cell-types occur here also, though they are not everywhere so clearly distinguishable as in the later stages. They conform closely in their characters to those of later stages, which are described in some detail, and so may be dealt with quite briefly here.

Of the two types, the pros. ect. cells (Pl. XII, figs. 70–72, *p.ect.*) are much the more numerous and the larger. They largely compose the superficial layer, and form a large proportion of the deep cells as well. Their cytoplasm tends to stain rather lightly, and is often vacuolated, whilst their nuclei are larger on the average and plumper-looking than those of the pr. end. cells, and they stain more lightly on the whole, the nuclear reticulum being eosinophil, though there is considerable variation in this respect, some of them having stained intensely black throughout.

The pr. end. cells (Pl. XII, figs. 70, 71, 72, *pr.end.*), much less numerous, are fairly easily recognizable by their relatively small size ( $\pm 0.0015 \times 0.013$  mm. in diameter), their mostly rounded or oval form and their rather deeply staining cytoplasm little if at all vacuolated. The nucleus is small (mostly round about  $0.006 \times 0.005$  mm. in diameter) and deeply staining, and tends to be rather less regular in form than that of the pros. ect. cells. It possesses a basophil reticulum and numbers of nucleolar granules of varying size.

The examples of pr. end. cells illustrated in Pl. XII, figs. 70, 71 and 72 (*pr.end.*) should be compared with those appearing in Pl. XIII, figs. 78, 79 and 80 of VVH 47. The irregularly quadrangular cell ( $0.015 \times 0.013$  mm. in diameter) in Pl. XII, fig. 72 (*emc.*) with deeply staining granular cytoplasm and a basophil nucleus ( $0.008 \times 0.0065$  mm. in diameter) with numerous coarse nucleolar granules disposed below its nuclear membrane, may be an endodermal mother-cell (*v.* p. 60 and Pl. XIII, fig. 82, of VVH 47).

*Yolk-bed cells.*—At least five such cells are present below the peripheral region of the disc, one lying 0.15 mm. within the margin. Two are uninucleate, two binucleate, and one trinucleate, the nuclei being in all strongly eosinophil. Their cytoplasmic bodies are poorly developed.

*Germ-ring.*—The germ-ring (Pl. XII, figs. 73 & 74, *gr.*) is well developed. It has a maximum width of about 0.136 mm. and a maximum thickness, adjacent to the disc-margin, of about 0.039 mm. It consists of a denser superficial zone, slightly vacuolated and rather thin, which passes over below into a light staining reticular zone enclosing sparse fine yolk-granules, and in its deeper part numbers of yolk-spheres of varying size. This reticular zone is traceable inwards below the disc-margin for a distance varying from 0.03 to 0.06 mm. The germ-ring, on reaching the margin of the disc, may slope gently inwards (Pl. XII, fig. 73) or it may become depressed to form a more or less deep groove in which the peripheral cells are situated (Pl. XII, fig. 74).

VVH 47. (Pl. XII, fig. 77; Pl. XIII, figs. 75, 76, 78–83; Pl. XIV, figs. 84 & 85.)

(Diameter of egg, 5 mm. (fresh), 6.17 mm. (after fixation). Diameter of ovum, 4.34 mm. Blastoderm, diameter in alcohol,  $1.09 \times 1.04$  mm., in section,  $0.99 \times 0.98$  mm. Thickness, 0.036 mm. Fixation, FBA.)

This blastoderm (Pl. XIII, fig. 75), though somewhat atypical in respect of its margin, is of great value, and the serial sections are excellent. It is of much the same size as that of *Ech.* 30, but differs from it in being roughly circular in form, and in its much less regular outline. Its periphery, though fairly well defined over the greater part of its extent, is more uneven and wavy than that of *Ech.* 30, and over the lower half of its right margin (in Pl. XIII, fig. 75) is decidedly ragged and irregular. Examination of the sections indicates that this is due to irregularities in the size and character of the peripheral cells in this region.

Pl. XIII, fig. 76 illustrates a section passing approximately through the centre of the blastoderm. It will be seen that as in *Ech.* 30 it is distinguishable into a thicker central and a thinner peripheral region, and that the underlying yolk-bed is only very slightly depressed centrally.

The central region is of greater width than in *Ech.* 30, measuring about 0.41 mm., but it varies somewhat and is difficult to measure accurately, whilst the peripheral region has an average width of about 0.27 mm. The central region attains a thickness of about 0.36 mm. (exceptionally 0.39 mm.), but is mostly thinner than this, ranging down to 0.030 mm. It is mostly two cells deep, though occasionally three cells may be found superimposed. The superficial cells (oval, fusiform, or spheroidal) form a well-marked continuous layer (Pl. XIII, fig. 76, Pl. XII, fig. 77), whilst the deep cells, oval or rounded, are loosely arranged. The cells may be vacuolated and are almost entirely devoid of yolk-spheres.

The peripheral region in its more central portion consists simply of the superficial layer, with below it sparse deep cells, usually devoid of yolk (Pl. XIII, fig. 78), but in its marginal zone, as in *Ech.* 30, the cells vary very considerably in size and in their yolk-content in different parts of its extent. In places, the superficial cells continue out to the periphery without exhibiting any marked enlargement, though an occasional cell may contain fine basophil yolk-spheres, whilst



deep cells are only sparsely present (Pl. XIII, fig. 76). In other places, however, over a width of from three to five cells in from the margin, the superficial cells are enlarged and rich in intermingled basophil and eosinophil spheres of varying size. Frequently, also, much enlarged deep cells, up to  $0.056 \times 0.024$  mm. in diameter and crowded with eosinophil or basophil spheres or both, occur below the peripheral cells which themselves may or may not contain yolk (Pl. XIV, figs. 84 & 85). Where such deep cells are present, the margin may reach a thickness of 0.033 mm.

The actual peripheral cells likewise vary greatly in size and in yolk-content. They may remain small, and may either be yolk-free (Pl. XIII, fig. 83) or contain small basophil spheres, but frequently they are large (up to  $0.051 \times 0.030$  mm. in diameter) and rich in basophil or, more often, eosinophil spheres (Pl. XIV, fig. 85). The occurrence in the marginal region of this blastoderm of considerable numbers of such enlarged and relatively inert cells, is somewhat atypical, and seems likely to have impeded the symmetrical spreading of the blastoderm. Indeed, we attribute the irregular and in part ragged character of its margin, noted above, directly to their presence. In this connection it is perhaps not devoid of significance that the germ-ring, in areas where such cells are specially prominent, tends to be thinner and rather richer in eosinophil granules than in the regions where the peripheral cells are smaller and less yolk-rich.

In the marginal region a few deep cells have become more or less deeply imbedded in the infra-marginal portions of the germ-ring and yolk-bed, where they are evidently destined to undergo degeneration. Usually, when the periphery of the blastoderm is two cells thick, the deep cell indents the infra-marginal portion of the germ-ring more or less deeply, causing it to assume a gutter-like form, such as is seen in Pl. XIV, fig. 84. Here the deep cell, large ( $0.040 \times 0.026$  mm. in diameter, nucleus 0.009 mm.) and rich in basophil yolk-spheres, is overlain by a yolk-free superficial cell. It lies in a well-marked depression of the germ-ring, its under-surface making intimate contact with the same. Its outer end, however, is separated from the germ-ring by a slight space, and this is closed above by a narrow bridge formed by the union of the tapering extremity of the superficial cell with a ridge-like projection of the ring. An exaggeration of these relations can easily result in the deep cell becoming more or less completely buried. A good example of such a cell is seen in Pl. XIV, fig. 85 (*bdc.*). Here the buried cell is large ( $0.045 \times 0.033$  mm. in diameter, nucleus  $0.014 \times 0.012$  mm.) and rich in yolk-spheres, mainly eosinophil.

We have observed two other "buried" cells with very similar relations, one of them shrunken and degenerate-looking, and a third, 0.15 mm. within the margin, which lies sunk in the yolk-bed, practically down to the level of its upper surface. It also is degenerating.

Yolk-balls (Pl. XIII, figs. 79 & 81, *ybl.*) are numerous in this blastoderm, and may still be found connected with the yolk-bed. They are usually much vacuolated, and contain fine basophil yolk-spheres and granules. They may reach a diameter of up to  $0.024 \times 0.016$  mm.

*Constitution of the Blastoderm.*—As already indicated, the importance of this stage centres in the fact that it enables us to establish with a greater degree of certainty than was possible in *Ech.* 30, the existence in the blastoderm of

two types of cell, which are destined eventually to segregate to form the two primary germ-layers. But, while we can identify cells as belonging to one or other of the two types without any great difficulty, that is not to say we can refer each and every cell in this blastoderm to its type-group, for there remain many cells of whose groupings we cannot be quite certain.

The cells of the two categories are broadly characterized as follows :—

(a) *Prospective Ectodermal Cells*.—These cells are much more numerous and larger on the average than the pr. end. cells. The average diameter of 20 cells measured is  $0.022 \times 0.014$  mm., and of their nuclei  $0.0080 \times 0.0078$  mm. The cells range in diameter from  $0.030 \times 0.015$  mm. to  $0.015 \times 0.013$  mm., and their nuclei from  $0.010 \times 0.009$  mm. to  $0.007$  mm. The cells (Pl. XIII, figs. 78–81, *p.ect.*) vary in shape; they are mostly fusiform, oval or elliptical, but may be oblong or rounded, and occur both in the superficial layer and deep thereto. The cytoplasm is finely granular, is often vacuolated, and stains on the whole less deeply than that of the pr. end. cells. In the peripheral region especially, the cells may be rich in basophil or eosinophil yolk-spheres. The nucleus is on the average larger, and stains less deeply than that of the pr. end. cells. It contains either one large basophil nucleolus (sometimes obviously composite) of variable, mostly irregular, shape or a number of smaller nucleoli (up to four or more) of varying size. The nuclear reticulum, usually not very conspicuous, is eosinophil, and has distributed through it numbers of fine basophil or eosinophil granules. Many cells, which from their size and cytoplasmic characters presumably belong to this category, possess nuclei which are deeply basophil throughout.

(b) *Primitive Endoderm Cells*.—Cells belonging to this category are much less numerous, more deeply staining, and on the average smaller than the pros. ect. cells. The average diameter of 16 cells measured is  $0.018 \times 0.013$  mm., that of their nuclei  $0.0060 \times 0.0057$  mm. The cells range in diameter from  $0.022 \times 0.017$  mm. to  $0.015 \times 0.012$  mm., and their nuclei from  $0.0075 \times 0.006$  mm. to  $0.006 \times 0.0045$  mm.

The cells (Pl. XIII, figs. 79–81, *pr. end.*) occur intermingled with the pros. ect. cells, and are oval, elliptical, oblong or rounded in form. The cytoplasm is finely granular, the granules tending to be slightly coarser and if anything rather more dispersed than those of the pros. ect. cells. They stain rather more deeply, and of a duller tint with eosin than those of the latter, often appearing slightly basophil, and sparse definitely basophil granules are sometimes interspersed among them. There is, however, some variation in the staining reactions of the pr. end. cells, for in a few cells which we judge belong to this category the cytoplasm stains no more deeply than that of pros. ect. cells. The cytoplasm may contain one or two large vacuoles, but on the whole it is much less subject to vacuolation than is that of the pros. ect. cells, and in contrast with the latter, and rather unexpectedly so, cells of this category only rarely contain yolk-spheres.

The nucleus exhibits certain characteristic features. It is definitely smaller on the average than that of the pros. ect. cell, and stains much more deeply, tending to be basophil throughout. It possesses numerous nucleolar granules varying in size from coarse to fine, many of them being disposed close below or in contact with the nuclear membrane. The nuclear reticulum is distinct and



prominent, and though it may be eosinophilic like that of the pros. ect. nucleus, it stains more intensely. The nucleus often appears less regular and more angular in contour than that of the pros. ect. cell, the outline of which (oval or spheroidal) is usually perfectly plump and smooth.

*Mitoses.*—Mitotic activity amongst the cells of the blastoderm is quite well marked. We have recorded and measured some 19 cells in the various phases of division, and though it is difficult to apportion these with certainty to their categories, since the cytoplasm of the dividing cell tends to stain more deeply than that of the resting cell, and size by itself is not a very reliable criterion, we judge that out of the 19, 10 are pros. ect. cells and 9 pr. end. cells. In addition we have recorded 10 pairs of sister-cells with telophase chromosome groups, of which half seem to belong to the one category and half to the other. It would therefore appear that mitotic activity is fairly equally distributed between the two categories of cell, but it should be remembered that the pros. ect. cells are much more numerous than the pr. end. cells.

We have also observed the occurrence, in four instances, of pr. end. cells in pairs, evidently sister-cells in which the nuclei have become fully reconstituted. One member of such a pair is seen on the right in Pl. XIII, fig. 79 (*pr. end.*), the other member being present in the preceding section.

In view of the above findings, we have made a careful search for the progenitors of the pr. end. cells (endodermal mother-cells), but with rather inconclusive results, though we suggest that cells of the type seen in Pl. XIII, figs. 81 & 82 (*emc.*) may possibly be such. The cells in question are moderately large, varying round about  $0.022 \times 0.016$  mm. in diameter, whilst the nucleus relatively to the cell-body appears small, its diameter ranging round about 0.0075 mm. The cytoplasm is similar to that of the pr. end. cells, being granular and deeply staining. The nucleus likewise stains deeply, being strongly basophil. The nuclear reticulum is well marked, and in it are present several larger nucleoli together with numbers of smaller peripherally situated granules. Cells of this type are not very numerous. They differ from pros. ect. cells with basophil nuclei, and of the same approximate size, in the more deeply staining character of their cytoplasm, and in possessing smaller nuclei.

No yolk-bed cells were seen.

*Germ-ring.*—The germ-ring (Pl. XIII, fig. 83; Pl. XIV, figs. 84 & 85, *gr.*) is not so well developed as in *Ech.* 30, and varies very considerably both in width and in thickness throughout its extent. Its maximum width is about 0.18 mm., and its thickness adjacent to the disc-margin may reach 0.018 mm. (or even more in minute localized patches); but it is mostly thinner, and this is usually the case where the marginal cells are large and rich in eosinophil yolk-spheres (Pl. XIV, fig. 85, *gr.*). The cytoplasm stains lightly with eosin, and presents a granular aspect owing to the presence in it of minute lightly eosinophil granules. The nuclei, also eosinophil, are fairly numerous, and are widely distributed throughout the inner half of the ring. Many of them are large (up to  $0.021 \times 0.013$  mm. in diameter), but others are quite small.

The connection of the peripheral cells with the germ-ring may be effected by the intimate adhesion of the under-surface of the cell in whole or in part with the surface of the ring, which is frequently slightly depressed over the area of apposition,

or the outer end of the cell may take the form of a tapering process which is attached either directly to the surface of the ring (Pl. XIII, fig. 83) or to a ridge-like projection from it when the ring is depressed for the reception of a peripheral deep cell (Pl. XIV, fig. 84). In one instance, the periphery being two cells thick, the germ-ring itself is produced into a minute vacuolated process with a bulbous end which makes contact with the peripheral superficial cell as in Pl. XII, fig. 74 of *Ech.* 30. In another exceptional case, the peripheral deep cell alone makes contact by its undersurface with the germ-ring, the superficial cell failing to make any connection with it.

VVH 45. (Pl. XIV, figs. 86 *a*, 86 *b*, 86 *c*, 87; Pl. XV, figs. 88–90.)

(Diameter of egg, 4.5 mm. (fresh), 4.5 mm. (after fixation). Diameter of ovum, 4.16 mm. Blastoderm, diameter in alcohol,  $1.5 \times 1.45$  mm., in section,  $1.38 \times 1.30$  (approximately) \*. Thickness, 0.032 mm. Fixation, FBA.)

The blastoderm, distinctly larger than that of VVH 47, is practically circular in outline, and in marked contrast with the latter possesses a sharply defined, perfectly regular rim as in that of VVH 6 (Pl. XV, fig. 91), which it essentially resembles. In its central region is a light circular patch which corresponds to the thicker central part of the blastoderm and the underlying fine-grained zone of the yolk-bed. The diameter of this zone is about 0.030 mm., that of the thicker central region of the blastoderm in Pl. XIV, fig. 87, varies from about 0.018 mm. to 0.027 mm.

The central region of the blastoderm is very variable in its constitution. In places it is only one cell thick, where it is formed by the superficial layer alone (Pl. XIV, fig. 86 *a*, Pl. XV, fig. 88); very exceptionally three cells may be found superimposed, but usually, where deep cells are present, it is two cells thick (Pl. XIV, fig. 87). The deep cells may occur singly, in small groups, or as a more or less connected sheet of up to 8–10 cells (Pl. XIV, fig. 87). They exhibit a tendency to apply themselves closely to the under-surface of the superficial layer, and there are many places where deep cells (usually singly, occasionally two together) have insinuated themselves into the superficial layer, or are in process of so doing (Pl. XIV, fig. 87, Pl. XV, figs. 88 & 90).

The superficial layer in the central region (Pl. XIV, figs. 86 *a* & 87, Pl. XV, fig. 88) is more variable in character, less well defined, and on the whole more attenuated than that of VVH 47. It is formed in the main of relatively thin, more or less elongated spindle-shaped cells, interspersed with which occur thicker cells, oval, elliptical or more or less rounded, whilst in many places, as just noted, deep cells are becoming intercalated in it (Pl. XV, fig. 88), a process which, as we shall see, is more accentuated in the succeeding stage VVH 6, and which culminates in the establishment of the unilaminar blastoderm, characteristic of the members of Group IV.

In the peripheral region (Pl. XIV, figs. 86 *b* & 86 *c*, Pl. XV, fig. 90) the superficial layer is very similar to that of the central region, except that some of the pros. ect. cells, especially those adjacent to the margin, may contain yolk-spheres. Deep cells are only sparsely present, though they are more numerous close to the

\* In this and the succeeding blastoderms we were unable to measure the curvature precisely, so that the measurements given are to be regarded as approximate only.



central region, and may occur here in small groups. Some of them contain fine basophil yolk-spheres. Cells in process of becoming intercalated are also met with (Pl. XV, fig. 90). At the margin, over a width of a few cells, there are places where the superficial pros. ect. cells are markedly enlarged and rich in basophil yolk-spheres, and the same may hold true for the underlying deep cells. But the structural details of the marginal region vary greatly from place to place, and even on opposite sides of the same section. For instance, in Pl. XIV, fig. 86 c, the cells of the superficial layer are only slightly enlarged over a width of three cells, whereas on the opposite side of the section they are markedly thickened and rich in yolk over a width of six or seven cells.

The actual peripheral cells similarly vary greatly from large yolk-rich cells up to  $0.048 \times 0.040$  mm. in diameter to small yolk-free cells of less than half that diameter. They rest in a more or less continuous groove on the surface of the germ-ring, of variable depth, and bounded on its outer side by a slight projecting rim (Pl. XIV, fig. 86 c). The under and outer surfaces of the peripheral cell mostly lie in close apposition with the surface of the groove, though sometimes the outer surface of the cell is separated from it by a minute space roofed over by a thin process passing from the cell to join the rim of the groove.

*Degenerate deep cells.*—Below the superficial layer, in the peripheral region of the blastoderm especially, isolated cells, mostly of large size and oval or rounded in form, are met with which exhibit varying degrees of degenerative change (Pl. XIV, fig. 86 b, *dgc.*). Some six or more are present, ranging in diameter from  $0.016 \times 0.012$  mm. to  $0.030 \times 0.024$  mm. The latter cell is oval, possesses glassy-looking darkly staining cytoplasm which is slightly vacuolated, and contains sparse basophil yolk-granules. Its nucleus is pycnotic.

*Yolk-bed nuclei.*—In the fine-grained central portion of the yolk-bed there are present about ten markedly eosinophil nuclei, of which six occur in one group, and the remainder, singly or in twos (Pl. XIV, fig. 87, Pl. XV, fig. 88, *ybn.*). It is not possible to distinguish cytoplasm around these nuclei, but in some cases the fine yolk surrounding them appears altered. Its yolk-granules have lost their sharp contours, and are eosinophil, in sharp contrast with the surrounding basophil spheres.

*Constitution of the Blastoderm.*—The constituent cells of the blastoderm, the pros. ect. cells and the pr. end. cells, closely conform in their characters to those of VVH 47, and need not be described in any detail.

The pros. ect. cells are still by far the more numerous and the larger of the two types. They predominate in the superficial layer, and also occur as deep cells, whilst others occupy an intermediate position and are in process of insinuating themselves into the superficial layer (Pl. XV, fig. 88 & 90). They vary in shape, being mostly fusiform or oval in the superficial layer, whilst deep cells may be oblong, oval or rounded. They also vary in size, but are definitely larger on the average than the pr. end. cells. The average diameter of 20 cells measured is  $0.022 \times 0.013$  mm., and that of their nuclei  $0.009 \times 0.008$  mm., the cells ranging in diameter from  $0.033 \times 0.018$  mm. to  $0.021 \times 0.009$  mm., and their nuclei from  $0.012 \times 0.011$  mm. to  $0.007$  mm. The cells are vacuolated in varying degree. In the central region the deep cells may contain minute eosinophil yolk-granules, whilst those at its periphery are often rich in fine basophil spheres; in the

peripheral region the cells, both superficial and deep, close to and at the margin, frequently enclose small basophil spheres.

The pr. end. cells have much the same shape and much the same dimensions as those of VVH 47, the average diameter of 24 cells measured being  $0.016 \times 0.010$  mm., and that of their nuclei  $0.006 \times 0.005$  mm. The cells range in diameter from  $0.018 \times 0.015$  mm. (nucleus  $0.0067$  mm.) to  $0.012 \times 0.009$  mm. (nucleus  $0.006 \times 0.005$  mm.). The cytoplasm usually stains more deeply than that of the pros. ect. cell, as also does the nucleus, which is basophil, though the nuclear reticulum tends to stain with eosin, but of a much darker tint than does that of the pros. ect. nucleus.

The cells are more individualized than the pros. ect. cells, since they mostly occur singly or in twos. They occur in the superficial layer both in the central (Pl. XIV, fig. 86 *a*, *pr.end.*) and peripheral regions, though in no great numbers, as well as deep to it (Pl. XIV, fig. 87, Pl. XV, fig. 89), and are also to be found insinuating themselves into it (Pl. XV, fig. 88, *emc.*).

In the blastoderm moderately large cells with deeply staining nuclei are met with in small numbers, which recall the cells in VVH 47, which we suggested might be of the nature of endodermal mother-cells. An example of such a cell is seen in Pl. XV, fig. 88 (*emc.*) on the right. It is becoming intercalated in the superficial layer and has a diameter of  $0.018 \times 0.016$  mm., nucleus  $0.0097 \times 0.008$  mm. Its cytoplasm has stained deeply, as has the nucleus, the reticulum of which has stained a dull red with eosin, and supports a large irregular nucleolus and numerous nucleolar granules.

*Mitoses.*—Mitotic activity is not quite so intense as in VVH 47, but is still considerable. We have recorded the measurements of some 20 cells in division, of which 14, with diameters ranging from  $0.021 \times 0.015$  mm. to  $0.018 \times 0.012$  mm., may be pros. ect. cells or endodermal mother-cells, whilst six with a diameter of  $\pm 0.015 \times 0.012$  mm. are possibly pr. end. cells (Pl. XV, fig. 89, *pr.end.*).

In addition, we have observed four pairs of sister-cells with telophase chromosome groups (one of the pairs lying actually at the periphery of the blastoderm) and one pair with the daughter-nuclei becoming reconstituted, all of which appear to be pr. end. cells. These records, such as they are, agree fairly well with those for VVH 47. Some excess of mitoses in the pros. ect. cells over those in the pr. end. cells is to be expected, in view of their numerical superiority.

*Germ-ring.*—The germ-ring (Pl. XIV, fig. 86 *c*) is well developed, and possesses a width (measured from the above-mentioned rim) of up to about  $0.064$  mm. and a maximum thickness varying from about  $0.024$  to  $0.032$  mm. It is traceable inwards below the margin of the blastoderm for a distance of about  $0.08$  mm. Its nuclei mostly occur singly in the sections, and measure up to  $0.024 \times 0.016$  mm. in diameter.

VVH 6. (Pl. XV, figs. 91, 92 *a, b, c*; Pl. XVI, figs. 93–96.)

(Diameter of egg,  $4.5$  mm. (fresh),  $5.51$  mm. (after fixation). Diameter of ovum,  $4.36$  mm. Blastoderm, diameter in alcohol,  $1.5 \times 1.45$  mm., in section,  $1.36 \times 1.38$  mm. (approximately). Thickness,  $0.032$  mm. Fixation, FBA.)



This blastoderm (Pl. XV, fig. 91) measured, in alcohol, has the same dimensions as that of VVH 45, but the sections show that it is definitely more advanced, inasmuch as it has made more striking progress towards the attainment of the unilaminar condition than has that stage. It is approximately circular in outline, and differs from VVH 45 only in slight details, *e. g.*, the larger size of the central light area which corresponds to the finer-grained central region of the yolk-bed, its rather more prominent margin and the presence of a very narrow smooth zone outside the latter, marking the site of the germ-ring.

In section the blastoderm is seen to have the same general structure and constitution as in VVH 45, but the features which characterize the central region of that stage are here markedly accentuated, as comparison of Pl. XV, fig. 92 *a* and Pl. XVI, fig. 93 of VVH 6 with Pl. XIV, figs. 86 *a* & 87 of VVH 45 demonstrates.

In VVH 45, as the figures show, the superficial layer in the central region is still fairly intact, though somewhat altered by the commencing immigration into it of deep cells. In VVH 6, on the other hand, it is clear from the figures that it can no longer be said to exist as a continuous, independent layer, though study of the sections shows that here and there short stretches of it are still recognizable. This striking change is the result of the intensification of the cell movements already initiated in VVH 45. Deep cells have not only crowded up and come to lie in close apposition with the under-surfaces of the superficial cells, but many of them have pushed in between the latter so as to reach the surface, and have thus become more or less completely intercalated amongst them.

As the outcome of all this activity, the arrangement of the cells of the blastoderm into a superficial layer and irregularly arranged deep cells, which is characteristic of the earlier stages included in this Group, has now given place in its central region to what we may describe as a laminar cell-aggregate comprising surface-cells and underlying deep cells, the latter all destined to become intercalated amongst the former, with the eventual formation of the unilaminar condition of the blastoderm which is distinctive of the members of the succeeding Group IV.

The general structure of the blastoderm is illustrated in Pl. XVI, fig. 93, showing the central region in a section just to one side of its centre, and in Pl. XV, fig. 92 *a, b, c*, depicting the central and the peripheral region on one side in a section passing approximately through the centre of the blastoderm, whilst structural details are shown under higher magnification in Pl. XVI, figs. 94 & 95.

The central region varies in width from about 0.39 mm. in Pl. XVI, fig. 93 to 0.24 mm. in Pl. XV, fig. 92 *a*, and it also varies somewhat in thickness, its maximum being about 0.032 mm. Mostly it is two cells thick, though occasionally three cells occur superimposed, and there are places where deep cells are absent, the spaces thus left being roofed over by surface-cells.

The surface-cells vary considerably in form and in size, since they include the original superficial cells as well as numbers of deep cells which have migrated up and have become, or are in process of becoming, intercalated between them. Nowhere in the central region can they be said to form an independent layer, though oval and fusiform cells, such as are found in the original layer, are more evident in some sections than in others (*cf.* Pl. XVI, fig. 93 with Pl. XV, fig. 92 *a*),

and here and there short connected stretches of up to eight such cells may be encountered. The majority of the surface-cells belong to the prospective ectoderm category. They are mostly large, and oval, fusiform or oblong in form; they stain lightly and are often coarsely vacuolated. Others of the surface cells, smaller and oval, oblong, or spheroidal in form, and more deeply staining, are primitive endoderm cells (Pl. XVI, fig. 94). Yet other cells in process of becoming intercalated, reach the surface only by a small part of their cell-body, or may just fail to do so (Pl. XVI, fig. 95).

The deep cells are likewise very variable in their form and size. They show no regular arrangement and may be compactly or loosely grouped. They tend to lie in close contact with the surface-cells, and indeed are frequently to be found insinuating themselves between the latter (Pl. XVI, fig. 95). The larger cells (pros. ect. cells), like those at the surface, are frequently coarsely vacuolated, a condition which tends to obscure their boundaries, but only rarely in the central region do they contain yolk-spheres.

The peripheral region of the blastoderm (Pl. XV, fig. 92 *b* and *c*) generally resembles that of the preceding stage, and consists of a continuous layer of superficial cells with sparse deep cells applied to its under-surface or in process of becoming intercalated in it. In the marginal zone especially, many of its constituent pros. ect. cells are rich in yolk-spheres, and may attain a considerable size (up to  $0.03 \times 0.018$  mm., nucleus  $0.009 \times 0.0075$  mm.), and the same holds true for such deep pros. ect. cells as occur in this same zone. But deep cells are by no means numerous in the peripheral region, and in individual sections it is rare to encounter more than three or four on either side of the central region. They are to be met with right out in the marginal zone, and in one or two instances underlie the peripheral cells. In one such case the deep cell has the characters of a pr. end. cell. It is pear-shaped, its narrow end taking the form of a slender peripherally directed process. Deep cells (both pros. ect. and pr. end. cells) in process of becoming intercalated in the superficial layer are not uncommon.

The actual peripheral cells (Pl. XV, fig. 92 *c*) are, as usual, very variable in their size and characters. They range in size from a fusiform cell  $0.042 \times 0.0097$  mm. in diameter, nucleus  $0.11 \times 0.009$  mm. down to a small oblong cell  $0.015 \times 0.009$  mm. in diameter, nucleus  $0.008 \times 0.006$  mm. This latter cell, as well as the corresponding cell on the opposite side which is only slightly larger, both possess deeply staining, yolk-free cytoplasm and a small basophil nucleus, and appear to be pr. end. cells. The peripheral pros. ect. cells usually contain more or less numerous basophil yolk-spheres. Only very rarely are they underlain by deep cells. The cells rest in a shallow groove on the surface of the germ-ring, about half their thickness or rather more projecting above the surface of the latter and over the area of contact, their limiting membranes are intimately fused with the egg-membrane covering it. In the outer end of the cell where it makes contact with the rim of the germ-ring groove there is fairly constantly present in the cytoplasm a small vacuolar space (Pl. XV, fig. 92 *c*), and similar spaces are sometimes present just above the lower surface of the cell as well.

*Degenerate cells.*—Amongst the deep cells in the central region and below the superficial layer in the peripheral region there occur here and there large oval or spheroidal cells (usually about  $0.016$ – $0.019$  mm. in diameter, but reaching in one



instance a diameter of  $0.032 \times 0.024$  mm.) which have undergone degenerative change (Pl. XV, fig. 92 *a*, Pl. XVI, fig. 93, *dgc.*). The cytoplasm is often vacuolated and usually eosinophil, and may contain a few fine basophil granules. The nucleus is more or less completely pycnotic. We have also observed an oval, vacuolated cell, obviously degenerate, lying between the blastoderm and the zona-albumen layer as well as a large degenerate cell ( $0.024 \times 0.018$  mm. in diameter and binucleate) buried below the yolk-membrane in the peripheral region.

*Yolk-balls.*—These structures (Pl. XV, fig. 92 *a*, Pl. XVI, fig. 93, *ybl.*) are remarkably abundant in this blastoderm, especially in the central region, and even occur between it and the zona-albumen layer. They vary in size from large to quite small, and also in character. Mostly they are delicate fragile-looking structures, much vacuolated and more or less rich in fine basophil yolk-granules, but they may be much more massive and crowded with small yolk-spheres of varying size. These coarser “balls” are very suggestive, at first sight, of masses of “free” yolk, and might even be mistaken for yolk-rich deep cells. They may reach a large size, one measuring as much as  $0.051 \times 0.025$  mm. in diameter.

*Constitution of the Blastoderm.*—The pros. ect. cells are in all essential respects similar to those of VVH 45. The average diameter of 20 cells measured is  $0.021 \times 0.011$  mm., that of their nuclei  $0.009 \times 0.008$  mm. The range in diameter of the cells is from  $0.027 \times 0.013$  mm. to  $0.018 \times 0.009$  mm. and of the nuclei from  $0.010 \times 0.009$  mm. to  $0.007$  mm., but superficial and deep cells in the peripheral region containing basophil yolk-spheres may be still larger.

The average diameter of ten cells in mitosis is  $0.025 \times 0.012$  mm.

The cells are mostly fusiform, oval or oblong in form. The finely granular cytoplasm is often coarsely vacuolated, especially in the case of deep cells, and stains rather lightly, though cells with fairly deep staining cytoplasm are not uncommon. In the central region the cells rarely contain yolk, but in the peripheral region they may be rich in small basophil spheres. The nucleus is large, oval or spheroidal in form and typically eosinophil, with a clear light staining reticulum, supporting a variable number of coarse basophil nucleolar granules; but darker staining basophil nuclei also occur, in which case the only criteria for distinguishing the cell as prospective ectodermal are its size and the diameter of the nucleus. It is, however, often difficult to decide to which of the two categories a particular cell with a basophil nucleus belongs.

The pr. end. cells (Pl. XV, fig. 92 *a*, Pl. XVI, figs. 93 & 94, *pr.end.*) also agree in all essential respects with those of VVH 45, but are slightly smaller, the average diameter of 20 cells measured being  $0.0148 \times 0.010$  mm., that of their nuclei  $0.006 \times 0.005$  mm. The range in diameter of the cells is from  $0.018 \times 0.012$  mm. to  $0.012 \times 0.010$  mm. and of the nuclei from  $0.009 \times 0.006$  mm. to  $0.005 \times 0.004$  mm.

The average diameter of eight cells in division is  $0.015 \times 0.011$  mm.

As the measurements show, they are distinctly smaller than the pros. ect. cells, and they stain on the whole much more deeply than the latter. They are also more variable in shape, since they may be oval, oblong, spheroidal, triangular or irregularly quadrangular in outline, and they are also more

individualized than the pros. ect. cells, whose outlines are sometimes difficult to determine.

Their cytoplasm is usually finely granular, and in the majority of the cells stains deeply, but cells with quite deeply staining cytoplasm, which is not obviously granular, also occur (Pl. XVI, fig. 95, *pr.end.*), as well as cells with light staining, granular cytoplasm. Sometimes it is slightly vacuolated, but on the whole vacuolation is less marked than in the pros. ect. cells, and yolk-spheres are rarely present.

The nucleus, oval or spheroidal, is typically small, and stains more deeply than that of the pros. ect. cell. Sometimes it is definitely basophil throughout, but frequently the nuclear reticulum simply stains a much darker tint with eosin than does that of the pros. ect. nucleus. Its nucleolar content is very variable, and may comprise one to several larger granules and a variable number of smaller, or the nucleus may be of the granular type with one or two larger granules centrally situated and numerous fine granules disposed mainly below the nuclear membrane.

Pr. end. cells are to be found intercalated amongst the surface pros. ect. cells (Pl. XVI, fig. 94, *pr.end.*), in process of intercalation between the latter (Pl. XVI, fig. 95) and as deep cells (Pl. XV, fig. 92 *a* and Pl. XVI, fig. 93). In view of the amoeboid activity displayed by these cells in later stages included in Group V, it is of interest that already in this stage we have encountered a number of cells in which the part of the cell-body which has reached, or is in process of reaching towards the surface, takes the form of a more or less definite process, sometimes conical as in the cell (*pr.end.*), seen in Pl. XVI, fig. 95.

*Endodermal Mother-cells.*—In this blastoderm, as in VVH 47 and 45, there is again present a type of cell which, judged by the dimensions of the cell-body and nucleus, should belong to the pros. ect. category, but which in cytoplasmic and nuclear characters more approximates to the pr. end. type. We have suggested they may be endodermal mother-cells. They vary in diameter from  $0.024 \times 0.015$  mm. to  $0.018 \times 0.010$  mm. or less, and their nuclei from  $0.011 \times 0.009$  mm. to  $0.0097 \times 0.008$  mm. The cytoplasm is granular, usually stains rather deeply, and may contain one or two large vacuoles. In one instance a few fine basophil yolk-spheres are present in it. The nucleus is large, basophil, and of the granular type.

*Mitoses.*—Mitotic activity is considerable in both categories of cell throughout the blastoderm. Cells, both surface and deep, in all phases of mitosis are frequently met with, and in addition pairs of spheroidal sister-cells with nuclei recently reconstituted or in process of becoming so are present in fair numbers both at the surface and deep thereto. We have measured some six pairs taken at random, and judging from their size four of these pairs with diameters round about  $0.012 \times 0.010$  mm. would seem to belong to the pr. end. category, and two pairs with diameters of about  $0.015 \times 0.010$  mm. to the pros. ect. category.

*Yolk-bed cells and nuclei.*—These attain a remarkable development in this egg. At least twenty-seven nuclei are present, mostly of large size. Ten of them are situated below the central region of the blastoderm, mostly towards its periphery, in contact with, or close below the yolk-membrane. Of these ten, four occur singly, two form a pair, and four occur in a group, of which two are seen in Pl. XVI.



fig. 93 (*ybn.*), with diameters of 0.018 and 0.016 mm. respectively. The remaining seventeen are situated in a large irregularly quadrangular mass of cytoplasm which lies just outside the periphery of the central region, its convexly bulging upper surface being invested by the barely distinguishable yolk-membrane (Pl. XVI, fig. 96, *ybn.*). It measures approximately 0.090 mm. in length  $\times$  0.064 mm. in width  $\times$  0.040 mm. in thickness. The cytoplasm is finely granular, slightly vacuolated, and distinctly eosinophil. The nuclei are distributed irregularly throughout the cytoplasm, and are mostly large, measuring up to  $0.018 \times 0.016$  mm. in diameter. Overlying this multinucleate formation, between it and the superficial layer of the blastoderm, is a slightly vacuolated eosinophil mass of homogeneous material, evidently of the nature of a coagulum, which is separated from the yolk-membrane covering the nucleated mass by a series of small vacuoles.

*Germ-ring.*—The germ-ring (Pl. XV, fig. 92 *c, gr.*) is well developed. Its width, measured from the slight rim bounding the groove on its surface, varies from 0.06 to 0.078 mm., whilst it is traceable inwards below the margin of the blastoderm for a distance of about 0.042 mm., so that its total maximum width is about 0.12 mm. It varies in maximum thickness from about 0.024 to 0.03 mm.

The number of nuclei present in individual sections varies from one to three. They are mostly large, varying in diameter from  $0.012 \times 0.009$  mm. to  $0.021 \times 0.016$  mm., and usually lie in the cytoplasm of the ring just outside the margin of the blastoderm, though occasionally they occur below the latter.

#### GROUP IV.

We include in this Group four eggs of *Echidna*, viz. VVH 32, VVH 42, *Echidna* VI and VVH 25, of which only the two former, with blastoderms 2.97 mm. and 3.28 mm. in diameter respectively, appear to be perfectly normal. The two latter ought to be in Group V, for *Echidna* VI possesses a blastoderm measuring in circumferential extent about 4.3 mm., whilst in VVH 25 the blastoderm is still larger, measuring about 6.3 mm. in circumferential extent. In both, the migratory capacity of the primitive endoderm cells seems to have been inhibited, and in spite of its growth, the blastoderm still remains unilaminar with the pr. end. cells intercalated in it, as in the two normal eggs.

The outstanding fact which study of this Group has established is that in the interval which separates its youngest member (VVH 32) from the most advanced stage in the preceding Group (VVH 6), the deep cells, which already in the latter had begun to push up between the surface-cells, have now completed that process of upward migration and have become intercalated in the single layer which constitutes the blastodermic membrane.

The blastoderm has thus become genuinely unilaminar, a highly remarkable and significant happening, constituting as it does the first step in the differentiation of the primary germ-layers, since it ensures that all the prospective ectodermal cells shall have reached their definitive position at the surface, and it only remains for the primitive endoderm cells to migrate out and acquire an internal position below them.

The occurrence of a unilaminar phase in the development of the Monotreme blastoderm was first recorded by Semon (1894). His observations are discussed below (p. 116).

VVH 32. (Pl. XVI, fig. 98; Pl. XVII, figs. 97, 99–103.)

(Diameter of egg, 5.0 mm. (fresh), 5.5 mm. (in formol). Diameter of ovum,  $4.4 \times 4.26$  mm. Blastoderm, diameter in alcohol,  $3.38 \times 3.16$  mm., in section about 2.9 mm. Fixation, FBA.)

As indicated above, this blastoderm exhibits a very striking advance both in size and structure on that of VVH 6, inasmuch as in the interval it has more than doubled in diameter and at the same time has advanced to the condition of a thin unilaminar membrane over its entire extent (Pl. XVI, fig. 98).

In surface view (Pl. XVII, fig. 97) the blastoderm is seen to be approximately circular in outline, with a regular well-defined rim. Centrally it shows the usual circular lightish area, slightly excentrically situated and corresponding to the underlying fine-grained zone of the yolk-bed.

In the sections the two types of cell composing the unilaminar blastoderm are for the most part readily distinguishable, though it is sometimes difficult to be certain to which category a particular cell belongs.

(a) The prospective ectodermal cells (Pl. XVI, fig. 98, Pl. XVII, fig. 99), still the more numerous and the larger of the two types, are rapidly assuming their definitive form. They vary in shape from oval with pointed ends to elongated spindle-shaped cells, more or less flattened and often reaching a large size, with their nuclei widely spaced. The cells on the average are of greater surface-extent but slightly thinner than those of VVH 6. The average diameter in 16 cells measured is  $0.028 \times 0.0075$  mm., the range in diameter being from  $0.015 \times 0.007$  mm. to  $0.036 \times 0.0067$  mm. The average diameter of 16 cells in division is slightly greater than that of the resting cell, being  $0.029 \times 0.009$  mm., the cells ranging in diameter from  $0.025 \times 0.009$  mm. to  $0.042 \times 0.008$  mm.

The nuclei are mostly oval or ellipsoidal in section, light-staining and of relatively large size. The average diameter in 50 measured is  $0.010 \times 0.0064$  mm., the range in diameter being from  $0.009 \times 0.006$  mm. to  $0.012 \times 0.009$  mm. They show no increase in volume over those of VVH 6 but have become more flattened.

At this stage, when the blastoderm may be presumed to be spreading fairly rapidly, considerable mitotic activity in the pros. ect. cells might well be expected, but it is not very marked.

(b) The primitive endoderm cells occur irregularly distributed amongst the pros. ect. cells throughout the extent of the blastodermic membrane, singly, in pairs and very occasionally in groups of three (Pl. XVI, fig. 98, Pl. XVII, figs. 100 & 102, *pr.end.*). They are present in considerable numbers, being definitely more numerous than in VVH 6, and are slightly larger on the average than those of the latter. The average diameter in 35 cells measured is  $0.0177 \times 0.0083$  mm., and that of their nuclei  $0.0078 \times 0.0067$  mm. The cells range in diameter from  $0.012 \times 0.009$  mm. to  $0.025 \times 0.009$  mm., and the nuclei from  $0.006 \times 0.004$  mm. to  $0.011 \times 0.0097$  mm. Out of the 35 cells measured, 23 possessed nuclei with a combined diameter of 0.014 mm. and over, and 12 of 0.013 mm. and under. The latter are presumably young cells, the nuclei of which have not yet attained their full size. Large cells possessing nuclei with a combined diameter of 0.017 mm. and over, of which 10 are included in the 35, may possibly belong to the category of endodermal mother-cells to which we have referred in preceding stages (*cf.* the



large cell on the right in Pl. XVII, fig. 99 (*emc.*) and the irregularly quadrangular cell in Pl. XVII, fig. 101 (*emc.*)).

The *pr. end.* cells exhibit the same distinctive characters as those of the preceding blastoderms. They mostly appear oval in section with rounded or pointed ends (Pl. XVII, fig. 100), but may be oblong, irregularly quadrangular (Pl. XVII, fig. 101, *emc.*) or spheroidal (Pl. XVII, fig. 102), and their junctions with adjoining cells are usually clear-cut and distinct.

As indicated above, the cells lie intercalated amongst the *pros. ect.* cells, wholly or partially in contact with the under-surface of the zona-albumen layer; but already there are indications that some of them are beginning to free themselves preparatory to acquiring their definitive deep position below the blastodermic membrane.

There is, however, no evidence as yet of active migration, and the very few cells we have observed in the deep position are daughter-cells, which have resulted from the division of intercalated mother-cells in planes oblique to the surface. In Pl. XVII, fig. 103 (*pr. end.*) is illustrated a condition we have several times encountered. Here a darkly stained cell in the prophase of division ( $0.015 \times 0.008$  mm. in diameter) lies in contact with the zona-albumen layer only over the mid-region of its cell-body, whilst its peripheral region is overlapped by the margins of the adjoining ectodermal cells. In all such cases, the *pr. end.* cell can acquire its deep position more or less passively, simply by the extension above it of the margins of the adjoining *pros. ect.* cells and their subsequent fusion.

That the *pr. end.* cells divide actively whilst still intercalated in the blastodermic membrane is shown by the occurrence in considerable numbers, of immature cells with nuclei under the average size, of pairs of sister-cells in fair numbers (Pl. XVII, fig. 100, *pr. end.*), and of cells actually in mitosis (Pl. XVII, fig. 103, *pr. end.*). From a detailed study of the series we conclude that a considerable increase in the number of *pr. end.* cells has been effected in the interval between this and the preceding stage.

In the marginal region the peripheral cells as usual vary considerably in size. They may be small and yolk-free or large (up to  $0.030 \times 0.018$  mm. in diameter) and contain a few small yolk-spheres. In a few instances, the actual peripheral cell has the characters of a primitive endoderm cell. The adjoining ectodermal cells of the marginal region are correspondingly variable but their yolk-content is now very considerably reduced, as compared with that in preceding stages.

The yolk-balls in this blastoderm are small and not numerous.

*Degenerate cells.*—These are common. They may lie intercalated in the blastoderm, in contact with the zona-albumen layer, or below the blastoderm or between it and the latter layer.

They are mostly oval or ellipsoidal in form, occur singly, or several (up to three) may be found together, and attain a diameter of up to  $0.036 \times 0.015$  mm. They are mostly markedly eosinophilic, with homogeneous cytoplasm often containing basophil granules. The nucleus is usually pycnotic.

In one section two large binucleate cells (one with a diameter of  $0.039 \times 0.022$  mm. and containing minute yolk-spheres) are present between the blastoderm and the zona-albumen layer.

*Germ-ring.*—The germ-ring is well developed, with a width outwards of up to about 0.10 mm. and a thickness varying from about 0.015 mm. to 0.024 mm. It may extend inwards for a distance of 0.010 mm. below the margin of the blastoderm. Its cytoplasm is coarsely granular, vacuolated and deeply staining. Its nuclei mostly occur singly and attain a diameter of up to  $0.024 \times 0.009$  mm.

On its surface is a gutter-like depression overhung by a slight projecting shelf with which the peripheral cells of the blastoderm are connected.

*Yolk-bed nuclei.*—Eight at least of these nuclei are present, together with the very degenerate remains of another. They lie close below the surface of the yolk-bed, two in its central region, the others in its periphery. They reach a diameter of up to  $0.021 \times 0.018$  mm., are all markedly eosinophilic, and in some of them the nuclear membrane is shrivelled and irregular.

VVH 42. (Pl. XVII, figs. 104 & 105; Pl. XVIII, figs. 106–111.)

(Diameter of egg, 4.7 mm. (fresh), 5.8 mm. (in formol). Diameter of ovum, 4.7 mm. Blastoderm, diameter in alcohol,  $3.36 \times 3.22$  mm., in section about 3.28 mm. Fixation, FBA.)

This blastoderm is practically a duplicate of VVH 32, with only some slight differences in detail. It is very similar in appearance and very much of the same size. Its unilaminar character is well brought out in Pl. XVII, figs. 104 & 105.

(a) *Prospective ectodermal cells.*—The majority of the pros. ect. cells have the form of large, flattened spindle-shaped cells (Pl. XVII, fig. 104), with their nuclei widely spaced; the remainder are smaller, oval in form with pointed ends and set closely together (Pl. XVII, fig. 105, left side). The cytoplasm stains rather lightly, is very finely granular and reticular or alveolar in character. The nucleus also tends to stain lightly and contains one or two, sometimes several, rounded basophil nucleoli, usually quite separate but sometimes aggregated into a single mass. The nuclear reticulum is delicate, eosinophil and bears very fine eosinophil granules.

The nuclei are mostly of a flattened oval form in section but not infrequently are ellipsoidal, and in the case of specially large cells may be spheroidal (Pl. XVIII, fig. 107, *p.ect.*). The average diameter of 36 nuclei measured is practically the same as in VVH 32, viz.  $0.010 \times 0.0056$  mm., the range being from  $0.009 \times 0.006$  mm. to  $0.012 \times 0.007$  mm. Exceptionally a pros. ect. cell may reach a diameter of  $0.042 \times 0.012$  mm., whilst cells with a long diameter of 0.030–0.033 mm. and a thickness of 0.009–0.012 mm. are not uncommon. In these large cells the nucleus may attain a diameter of  $0.012 \times 0.009$  mm. or even slightly more. Dividing cells tend to be large, six in the metaphase ranging from  $0.030 \times 0.009$  mm. to  $0.045 \times 0.0097$  mm. in diameter. In such cells the cytoplasm is more coarsely granular than that of the resting cell, but the granules are not usually so deeply staining as those of pr. end. cells in mitosis.

Pl. XVII, fig. 104 illustrates a small stretch of the blastoderm composed exclusively of pros. ect. cells, and Pl. XVII, fig. 105 another stretch in which the second cell on the right is a pr. end. cell (*pr.end.*).

(b) *Primitive endoderm cells.*—In this blastoderm these cells appear to be more numerous than in VVH 32, as the outcome of active mitotic division, which is still proceeding. As in VVH 32 they are distributed quite irregularly throughout the extent of the blastoderm, including its periphery. They are disposed singly



or in groups of two or three, rarely more, whilst pairs of sister-cells are not uncommon. They show the same variety in form as those of VVH 32, and may be fusiform, oval, oblong, pear-shaped or spheroidal (Pl. XVII, fig. 105, Pl. XVIII, figs. 106 & 109). They are plasma-rich, and with few exceptions stain much more deeply than the pros. ect. cells.

In size they also agree closely with those of VVH 32, the average diameter of the cell-body in 75 measured being  $0.0184 \times 0.0088$  mm. and of the nucleus  $0.0075 \times 0.0062$  mm. Out of the 75 cells measured, 34 possessed nuclei with a combined diameter of from 0.014 to 0.018 mm., whilst 41 had nuclei with a combined diameter of from 0.008 to 0.013 mm. The latter group includes cells in which the nuclei have not yet attained their full size, *i.e.* adolescent cells, and the fact that rather more than half of the cells measured belongs to this class, whereas in VVH 32 only about one-third of the cells measured is of this type, testifies to the very considerable mitotic activity on the part of the pr. end. cells which has gone on in this blastoderm. That it is still proceeding is evidenced by the relatively large number of cells encountered in actual process of division as well as by the occurrence of pairs of sister-cells in the telophase or with nuclei becoming reconstituted.

The average diameter of 15 cells in division is  $0.020 \times 0.009$  mm., the cells ranging from  $0.015 \times 0.007$  mm. to  $0.027 \times 0.012$  mm. in diameter.

As in VVH 32, though in less degree, there is evidence that some of the pr. end. cells are in progress of acquiring their deep position as the result of the growth over them of contiguous pros. ect. cells, but we have observed only one cell which seems to have completely lost contact with the zona-albumen layer and so become genuinely deep. The possibility, however, that this particular cell may be one which has failed to become intercalated, cannot altogether be excluded.

This blastoderm also provides some evidence that pr. end. cells may acquire the deep position as the result of the division of intercalated mother-cells in planes parallel with or oblique to the surface. In the oblong cell depicted in Pl. XVIII, fig. 109 (*pr.end.*<sup>1</sup>), the mitotic figure, cut somewhat obliquely, appears to be in the anaphase, the plane of division being oblique to the surface, so that the lowermost of the resulting two daughter-cells would automatically become deep.

Here again in this blastoderm, especially in its central region, we have encountered a number of fairly large cells well individualized and mostly ovoidal in form which are presumably endodermal mother-cells (Pl. XVIII, figs. 107 & 108, *emc.*).

The periphery of the blastoderm is formed for the most part by small cells, devoid of yolk-spheres. Some of them are in division and a few have the characters of pr. end. cells. Occasional pros. ect. cells in the marginal region contain small yolk-spheres, but, as in VVH 32, the yolk-content of the cells is now almost negligible, whilst yolk-balls also are small and not very common.

*Degenerate and abnormal cells.*—Degenerate cells, small (Pl. XVII, fig. 105, *dgc.*) as well as large (up to  $0.024 \times 0.018$  mm. in diameter), are fairly common below the blastoderm, as well as intercalated in it, and may also occur between it and the zona-albumen layer, but are not so numerous as in VVH 32. They are mostly oval or spheroidal, their cytoplasm, homogeneous or granular, is eosinophil, contains sparse basophil granules and is often vacuolated. The nucleus, when present, is pycnotic.

In addition to these obviously degenerate cells there are also present a few large bi- to multinucleate cells suggestive of greatly hypertrophied pr. end. cells, and likewise destined to degenerate. One such cell is seen in Pl. XVIII, fig. 110 (*dgc.*); the mid-region of its upper surface lies in contact with the zona-albumen layer, whilst its peripheral region is overlain by the adjoining pros. ect. cells. It has a diameter of  $0.042 \times 0.024$  mm. and possesses one large nucleus ( $0.012 \times 0.0067$  mm. in diameter) which is produced into a small bud and five much smaller accessory nuclei which may also have arisen as buds. The cytoplasm is granular and coarsely vacuolated. Three comparable but slightly smaller cells were also observed, two of them binucleate and one trinucleate.

*Yolk-bed nuclei.*—Only four such nuclei have been observed in the yolk-bed of this egg, of which one, peripherally situated, is small, flattened and shrivelled. The nucleus seen in Pl. XVIII, fig. 111 (*ybn.*) lies at the periphery of the fine-grained zone of the yolk-bed, the nuclear membrane over its upper surface being intimately united with the yolk-membrane. It is noteworthy for its huge size ( $0.027 \times 0.018$  mm. in diameter) and for the presence in its very granular reticulum of five eosinophil spheres, homogeneous in character and curiously suggestive of yolk-spheres.

*Germ-ring.*—This is well developed and possesses a width varying from about 0.075 to 0.11 mm. and a thickness of from about 0.015 to 0.021 mm. It consists of a thin, more compact, alveolar zone below the egg-membrane and a deep coarsely vacuolated zone containing large and small yolk-spheres. Its nuclei occur singly and measure up to  $0.024 \times 0.018$  mm. in diameter. Its marginal groove is rather shallower than that in VVH 32.

#### *Echidna* VI.

(Diameter of egg, 4.3 mm. (fresh),  $5.7 \times 5.8$  mm. (after fixation). Diameter of ovum,  $4.05 \times 4.16$  mm. Fixation, FBA.)

The blastoderm appears to have been complete in the intact egg but in the sections, owing to some defect in technique, its peripheral region is rather fragmented. Its circumferential extent measured in section is about 4.3 mm., and that of the remaining uncovered portion of the egg about 6.2 mm., the calculated circumference of the intact egg being 12.8 mm. It is unilaminar throughout its extent.

The pros. ect. cells conform to type. They are fusiform and mostly small. The average diameter of the nucleus in 20 measured is  $0.010 \times 0.0054$  mm. In the marginal region the cells often contain a few small yolk-spheres and occasionally the periphery may be two cells in thickness. The peripheral cells are attached to the ridge bounding the groove on the germ-ring by thin extensions of their cell-bodies.

From the surface-extent of the blastoderm we should have expected to find the pr. end. cells approaching the condition they have attained in *Echidna* IV of Group V. but so far as we have been able to observe none of them has reached the deep position. Moreover, relatively to the extent of the blastoderm, they are not nearly so numerous as they should be, and they present yet another curious feature, and that is that many of them, indeed an inordinate proportion, are in some phase of mitosis. Out of 48 pr. end. cells which we have listed, some 12 are nucleated, 16 are in the metaphase, four in later stages of mitosis, and 16 possess a central (telophase) group of chromosones.



In their dimensions they are slightly smaller than those of VVH 42, the average diameter of ten cells being  $0.017 \times 0.006$  mm. and that of their nuclei  $0.0068 \times 0.005$  mm.

The pr. end. cells evidently suffered from some inherent defect which inhibited their normal increase as well as their inward migration.

Degenerate cells with pycnotic nuclei are common. Yolk-balls are fairly numerous; they are mostly small and delicate, but a few large balls containing basophil yolk-spheres and measuring up to  $0.057 \times 0.027$  mm. in diameter are also present.

The germ-ring appears normal and well developed. It has a width outwards of about 0.06 mm. and an inward extension of about half that amount, whilst its thickness varies from about 0.021 mm. to 0.030 mm. Its nuclei are mostly basophilic and reach a diameter of up to  $0.025 \times 0.010$  mm.

#### VVH 25. (Pl. XVIII, figs. 112-114.)

(Diameter of egg, 4.0 mm. (fresh), 5.0 mm. (after fixation). Diameter of ovum, 4.13 mm. Blastoderm, approximate circumferential extent, measured in the sections, 6.3 mm., and of uncovered lower polar area about 4.0 mm. Fixation, FBA.)

The blastoderm, measured in the sections, has a circumferential extent of about 6.3 mm., whilst that of the uncovered lower polar area is about 4 mm., so that it extended well below the equator of the egg, and is definitely larger than that of the youngest member of Group V, *Echidna* IV, with a circumferential extent of about 5.5 mm.

As mentioned above, it is still unilaminar, no deep pr. end. cells being present, so far as we have observed. Moreover, in the sections, that part of the central region of the blastoderm which normally overlies the fine-grained zone of the yolk-bed is lacking over a width of about 1.2 mm. We have failed to find any remnants of the blastodermic membrane in the region of the defect, and as the sections are otherwise quite reasonably good, we conclude that this defect is not an artefact but the result of localized atrophy in the intact egg, which may well have adversely affected its normal development.

The pros. ect. cells (Pl. XVIII, fig. 112) appear to be normal, apart from the fact that some of them reach a large size; one huge cell, with sparse eosinophil yolk-spheres in its cytoplasm, reaching a diameter of  $0.081 \times 0.0097$  mm., nucleus  $0.016 \times 0.008$  mm.

The general appearance of the pros. ect. cells, as seen in tangential sections of the blastoderm, is illustrated in Pl. XVIII, fig. 114. In such sections we have observed two instances in which the cell-body is produced into a thin cytoplasmic process, quite like the processes given off by pr. end. cells in later stages.

In the peripheral region the cells occasionally contain small numbers of basophil or eosinophil yolk-spheres.

Pr. end. cells (Pl. XVIII, fig. 113, *pr.end.*) are present in fair numbers in the unilaminar blastoderm and are to be met with quite close to and actually at its margin. They are slightly smaller than those of VVH 42, the average diameter of 25 cells measured being  $0.016 \times 0.007$  mm., that of the nucleus  $0.007 \times 0.005$  mm.

There is evidence of considerable mitotic activity in both types of cell, and quite a large number of pairs of sister-cells has been observed (Pl. XVIII, fig. 114, right side). Pr. end. cells dividing in planes oblique to the surface are also met with.

*Degenerate cells.*—In addition to sparse cells with pycnotic nuclei of the type described in preceding stages, there are present a few large cells (up to  $0.057 \times 0.024$  mm. in diameter), either laden with eosinophil yolk-spheres or vacuolated and containing sparse basophil granules. One cell of the latter type and in the metaphase was observed outside the blastodermic membrane.

*Yolk-bed nuclei.*—At least nine are present, all of them eosinophil, more or less shrivelled and degenerate. Five of them (two large and three small) occur in one group, close below the yolk-membrane and just outside the fine-grained zone of the yolk-bed.

*Germ-ring.*—Over most of its extent the germ-ring is poorly developed. It consists of vacuolated cytoplasm, rather light staining and more granular than usual, enclosing sparse yolk-spheres. At its best it attains a thickness of about  $0.024$  mm., a width outwards of about  $0.045$ , and an inward continuation of about the same extent. Its nuclei occur singly, are eosinophil and vary in diameter from  $0.006 \times 0.005$  to  $0.021 \times 0.015$  mm.

#### GROUP V.

The material available for inclusion in this fifth and last Group comprises ten eggs of *Echidna* and two twin-eggs of *Platypus* (S and SS). Of these, the following nine in approximate order of age, viz. *Echidna* IV and XVIII, VVH 8, 3, 28, 11, *Echidna* I and *Platypus* S and SS, form an excellent overlapping series and are deserving of detailed description. The three remaining eggs, *Echidna* IX, TLB 1 and *Echidna* XII, exhibit individual points of interest and will be dealt with more briefly in an appendix to this section.

The material here described is of particular importance, since it enables us to complete our account of the formation of the primary germ-layers in the Monotremata and to show, for the first time, how the definitive bilaminar blastoderm (composed of a superficial layer of ectoderm and an underlying layer of endoderm) is derived from its unilaminar fore-runner. Furthermore, it enables us to demonstrate how the blastoderm during the differentiation of the primary germ-layers gradually extends peripherally over the yolk-mass of the egg, in continuity with and preceded by the germ-ring, and finally effects its complete enclosure, a cicatricial thickening, the so-called yolk-navel, at the lower pole of the egg, marking the last point of closure. In this way the originally solid egg becomes converted into a potential vesicular stage or blastocyst, capable of increasing in size and of absorbing the nutritive fluid secreted by the tubular glands in the uterine wall.

*Echidna* IV. (Pl. XIX, figs. 115–124, Pl. XX, figs. 125 & 126.)

(Diameter of egg,  $4.5$  mm. (fresh). Diameter of ovum,  $4.2 \times 4.1$  mm. Circumferential width of blastoderm, estimated as about  $5.5$  mm. Fixation, FBA.)

In the interval between this stage and VVH 42 of Group IV, marked progress has been made. Not only has the blastoderm increased considerably in surface-extent but the pr. end. cells have increased greatly in number, and many of them



have acquired their definitive deep position below the blastodermic membrane, though, as yet, relatively few of them possess cytoplasmic processes arising from their cell-bodies.

With the object of facilitating infiltration during imbedding, the lower portion of the ovum was removed, but in so doing the periphery of the blastoderm was slightly damaged on one side. Measurements of the sections show that on the undamaged side, the blastoderm, measured from the centre of the yolk-bed to the germ-ring, has a circumferential width of about 2.0 mm., whilst on the opposite side, measured from the same point to the cut edge of the blastoderm, the width is about 3.32 mm., thus revealing a curious lack of coincidence between the centre of the blastoderm and that of the yolk-bed, which we have also noticed in other eggs. The circumferential width of the blastoderm in the sections is thus about 5.32 mm., and we are probably not far out in assuming that in the intact egg it was about 5.5 mm., which compares with 3.28 mm. in VVH 42. The blastoderm accordingly must have extended almost to the equator of the egg.

*Prospective ectoderm cells.*—These cells (Pl. XIX, figs. 115 & 116) are now more uniform in character than those of VVH 42, being mostly large and thin and spindle-shaped in section. In the peripheral region some of the cells contain sparse small yolk-spheres.

The nucleus is oval to oblong in section and flattened. The average diameter of 36 measured in section is  $0.011 \times 0.0053$  mm., which compares with  $0.010 \times 0.0056$  mm. in VVH 42, whilst the average of 12 measured in surface view is  $0.011 \times 0.0097$  mm., so that they have roughly the form of flattened spheroids.

As usual they stain rather lightly like the cytoplasm, the nuclear reticulum being little prominent and lightly eosinophil, though deeply basophil nuclei do occur.

Cells in division are fairly numerous and are recognizable as ectodermal by their relatively large size and the finely granular character of their cytoplasm, the granulation being much more prominent than that of the resting cell.

The average diameter in 20 cells measured in varying phases of mitosis is  $0.029 \times 0.0067$  mm. They are distributed throughout the extent of the blastoderm and do not appear to be specially numerous in the peripheral region, so that growth in surface-extent would seem to affect the blastoderm as a whole and not any particular region. Some five pairs of daughter cells have been noted. They appear as small spindle-shaped cells with dark staining granular cytoplasm and small basophil nuclei of the granular type, about 0.006 mm. in diameter in recently formed pairs.

*Primitive endoderm cells.*—The pr. end. cells (Pl. XIX, figs. 116, 117, 118, *pr.end.*) are now much more numerous than in preceding stages. Moreover, as stated above, many of them have now migrated to their definitive deep position below the blastodermic membrane (Pl. XIX, figs. 116 & 117, *pr.end.*), whilst others still remain intercalated in the same (Pl. XIX, figs. 116 & 117), and yet others, more or less isolated but still in partial contact with the zona-albumen layer, are in process of migration (Pl. XIX, figs. 118 & 119).

The deep cells (Pl. XIX, figs. 116 & 117, *pr.end.*) lie in close contact with the under-surface of the blastodermic membrane and differ in no way structurally from the intercalated. They are mostly oval, ellipsoidal or spheroidal in form but may be oblong or, rarely, more or less fusiform, in which case one or both ends

of the cell may be continued as a short cytoplasmic process (Pl. XIX, figs. 119 & 120). They occur widely dispersed below the blastodermic membrane, mostly singly but not infrequently in twos, rarely more\* (Pl. XIX, fig. 116).

The intercalated cells, also, mostly occur singly, but groups of two or three cells as well as pairs of sister-cells are of fairly frequent occurrence (Pl. XIX, figs. 117 & 118), whilst small groups of three or four cells comprising both intercalated and deep (Pl. XIX, fig. 116) are not uncommon. The cells exhibit the same variety in form as the deep. They are distinctly thicker than the the pros. ect. cells, their cytoplasm stains more deeply than that of the latter, as do their nuclei which are less flattened, whilst their cell-bodies are more distinctly delimited. These features, together with their form, render their identification fairly easy. Though they are only slightly smaller on the average than those of VVH 42, their nuclei are definitely larger. The average diameter of 30 intercalated cells measured is  $0.017 \times 0.0083$  mm., whilst that of their nuclei is  $0.0093 \times 0.0069$  mm. as compared with  $0.0075 \times 0.0062$  mm. in VVH 42.

In 24 deep cells measured the average diameter proves to be precisely the same as that of the intercalated cells, and that of their nuclei practically the same ( $0.0092 \times 0.0073$  mm.). In surface view the average diameter of 21 cells (intercalated and deep) is  $0.015 \times 0.012$  mm., that of their nuclei  $0.009 \times 0.008$  mm.

The cytoplasm of the pr. end. cells is basophilic, tends to stain rather deeply and contains more or less distinct dispersed granules. Small vacuoles are frequently present in it and occasionally in the peripheral region, the cells contain one or two small yolk-spheres. The nucleus appears large relatively to the cell-body. It is oval to spheroidal in form and smaller and less flattened than the pros. ect. nucleus. It usually possesses two or three large basophil nucleoli, sometimes clumped into an angular mass, together with numerous minute granules dispersed throughout the nuclear reticulum. The latter is coarser than that of the pros. ect. nucleus, and stains a deeper tint with eosin, but nuclei which are intensely basophil throughout are not uncommon.

The intercalated cells typically lie in broad contact with the zona-albumen layer by their upper surfaces, whilst peripherally they are in contact with the surrounding pros. ect. cells or with each other, as in Pl. XIX, fig. 117, but their areas of contact with the zona-albumen layer may be much reduced by the ingrowth above them of the margins of adjoining pros. ect. cells, with the result that they become partially isolated (Pl. XIX, fig. 119). Such cells, as we have already seen, can readily acquire the deep position simply by the pros. ect. cells closing in over them and so completely cutting off their contact with the zona-albumen layer.

Many of the cells appear at first sight as if they were directly continuous with the adjoining ectodermal cells (Pl. XIX, figs. 119 & 122, *pr.end.*), but on more careful examination it can be seen that the limiting membrane of the cell continues uninterruptedly over the region of apparent continuity and that the relationship is merely one of close and intimate apposition. An even more deceptive appearance of continuity is produced in some instances where the thin margin of the pros. ect. cell overlaps a short process arising from the pr. end. cell, as in Pl. XIX,

\* In the Preliminary Communication (Flynn & Hill (1941)), the second sentence in the second paragraph on p. 248 has been misplaced. It refers to the intercalated cells, and should follow the first sentence in the third paragraph.



figs. 117 & 119. That the pr. end. cells maintain their independence throughout is further confirmed by the fact that in surface views, as seen in tangential sections, the outlines of the cells always appear sharp and distinct (Pl. XIX, fig. 124).

The evidence derivable from this and succeeding stages shows that the intercalated cells attain their deep position in three main ways. A partially isolated cell, as we have seen above, may become deep more or less passively by the adjoining ectodermal cells closing in over it. On the other hand, we have to recognize that the pr. end. cell itself is endowed with some power of amoeboid movement so that it is capable not only of altering its shape and migrating bodily but of giving origin to one or more cytoplasmic processes which, as later stages show, can anastomose with each other and are really of the nature of pseudopodia. Pl. XIX, figs. 119 & 122 provide two examples of this migratory capacity on the part of pr. end. cells. In each of these figures we see an intercalated cell which, whilst still in contact with the zona-albumen layer and with the margin of the pros. ect. cell adjoining it on one side, has slipped some way under the pros. ect. cell on the opposite side, and is evidently in process of acquiring the deep position. From this condition it is but a step to that illustrated in Pl. XIX, fig. 120, where the body of the intercalated cell is produced into a thick process (about 0.012 mm. in length) underlying the adjacent ectodermal cell. But it should be emphasized that in the present stage this migratory movement of the pr. end. cells would seem to be effected in the majority of the cells in the absence of definite cytoplasmic processes. Such processes, indeed, are only just beginning to appear (Pl. XIX, fig. 124). An exceptionally well developed process (about 0.010 mm. in length) is given off by the deep cell illustrated in Pl. XIX, fig. 121 (*pr.end.d.*), but the majority of the latter cells are still devoid of them, and we have encountered only a relatively small number of intercalated cells with distinct processes. Usually but a single one is given off from the cell, though we have observed a few fusiform deep cells with a slender process arising from each end of the cell-body. The processes may be quite short and prickly-like or more elongated (up to 0.015 mm. in length), slender and tapering (Pl. XIX, fig. 124, *pr.end.d.*). Their cytoplasm is usually distinguishable from that of the cell-body, being in most very finely vacuolated and more lightly staining than that of the latter, but it may be coarsely granular and deeply staining (Pl. XIX, fig. 121), whilst in the cell depicted in Pl. XIX, fig. 120, there is no clear distinction between the cytoplasm of the process and that of the cell-body. Judging from the present stage it would seem that the majority of the pr. end. cells give origin to their processes only after they have acquired the deep position.

Lastly in this connection, there is yet a third method by which a cell may acquire the deep position, and that is by the division of an intercalated mother-cell in a plane parallel with or oblique to the surface; the result being that the lowermost of the two daughter-cells gains the deep position (Pl. XIX, figs. 122 & 123).

Mitotic activity in the pr. end. cells is on an extensive scale, but is almost exclusively confined in the present stage to the intercalated cells, very few of the deep cells having been observed in division. The average diameter of 36 cells in mitosis is  $0.017 \times 0.010$  mm., the cells ranging in diameter from  $0.015 \times 0.009$  mm. to  $0.024 \times 0.012$  mm., whilst the average diameter of four

pairs of sister-cells in the telophase is  $0.011 \times 0.0087$  mm. Cells in division tend to stain rather deeply, the cytoplasm containing rather coarse basophil granules.

*Degenerate cells.*—Numbers of such cells are present both below the blastodermic membrane and intercalated in the same, and often reach a large size. Two are illustrated in Pl. XX, fig. 125 (*dgc.*). The cell on the left, in contact with the zona-albumen layer, has a diameter of  $0.038 \times 0.027$  mm., and that of its nucleus  $0.012 \times 0.009$  mm. Its cytoplasm is basophil, granular and vacuolated, and contains peripherally sparse small yolk-spheres. To the left of the nucleus is a dense, finely granular, intensely stained area suggestive of a centrosphere. The cell on the right is deep and has a diameter of  $0.039 \times 0.024$  mm. Its cytoplasm is vacuolated and contains numbers of small yolk-spheres. No nucleus was seen. In one section, a group of four cells is present, all with vacuolated cytoplasm, containing basophil granules and pycnotic nuclei, whilst in another, a large degenerate cell directly overlies the germ-ring.

*Germ-ring.*—The germ-ring (Pl. XX, fig. 126, *gr.*) varies in width from about 0.12 to 0.14 mm. and has a thickness at the level of the nuclei of about 0.015 mm., but elsewhere it is thin and altogether is less massive than usual. It consists of a thin darkly staining superficial layer, presenting a moniliform appearance owing to the presence in it, at intervals, of minute basophil granules and of an underlying lightly staining layer in which yolk-spheres are situated. Its nuclei occur singly in the sections, that in the section figured having a diameter of  $0.024 \times 0.012$  mm. The usual peripheral groove on its surface is here very shallow or absent, and the peripheral cells of the blastoderm are attached directly to its surface, each by a thin process, often hook-like in section, as in Pl. XX, fig. 126.

The peripheral cells are for the most part small and devoid of yolk, though in the marginal region, cells here and there may contain one or more small spheres.

*Yolk-bed nuclei.*—In this egg these appear to be absent.

#### *Echidna* XVIII. (Pl. XX, figs. 127–129.)

(Diameter of egg, 5.20 mm. (fresh),  $5.25 \times 5.0$  mm. (after fixation). Circumferential width of blastoderm about 7.9 mm., and of the uncovered lower polar area about 3.0 mm. Shell, 0.011 mm. in thickness. Fixation, Bouin.)

The egg was sectioned with the shell *in situ*. The blastoderm proves to be imperfect, its central region overlying the yolk-bed being absent over a width of about 1.6 mm. But apart from this defect it is fairly complete and is worthy of brief notice, especially as the tangential sections provide instructive surface views of the pr. end. cells, many of them being provided with pseudopodial processes which reach a higher degree of development than those of *Echidna* IV and equal, if indeed they do not excel, those of the succeeding stage VVH 8.

In its dimensions, as will be seen from the above measurements, the blastoderm is well in advance of *Echidna* IV, falling between that stage and VVH 8.

The pros. ect. cells generally resemble those of *Echidna* IV, being spindle-shaped and thin. The average diameter of 20 nuclei measured in surface view is much as in that stage, being  $0.010 \times 0.009$  mm.

The pr. end. cells, intercalated and deep, are fairly numerous. The average diameter of 15 cells measured in section is rather less than in *Echidna* IV, being  $0.014 \times 0.008$  mm. and that of their nuclei  $0.008 \times 0.007$  mm., but the average



diameter of 32 cells measured in surface view is somewhat greater, being  $0.017 \times 0.013$  mm. and that of their nuclei  $0.009 \times 0.0078$  mm., in close agreement with *Echidna* IV.

Seen in the transverse sections, the cells exhibit much the same variations in form that we encountered in *Echidna* IV, though intercalated pear-shaped cells, with the thin end prolonged into a pseudopodial process underlying an adjoining ectodermal cell, appear to be rather more numerous than in that stage.

But the true form of the pr. end. cells and their astonishing diversity in appearance only becomes apparent when they are seen in surface view in the tangential sections (Pl. XX, figs. 127-129). These figures bear striking testimony to the possession by the cells of amoeboid properties, as evidenced by their capacity to push out pseudopodial processes.

The cell-body may be more or less rounded or oval in outline and provided with one, two or more processes of varying length and thickness (Pl. XX, fig. 127) or fusiform with a process arising from each end, or it may be irregularly quadrangular with a process of very varying length and thickness arising from each angle, or again it may be triangular with a more or less elongated apical process and one or two basal processes (Pl. XX, fig. 129), or again it may present a stellate appearance owing to the presence of a number of short pointed processes (up to six in one case.)

Pl. XX, fig. 128 shows a curious type of cell with an elongated narrow body (about 0.027 mm. in length), swollen below to contain the nucleus and slightly expanded and obliquely truncated at its opposite end, where it is composed of rather lighter staining vacuolated cytoplasm. Here it gives origin to two processes, a short tapering process on the right and a long curved process on the left (about 0.030 mm. in length). This gives off a slender branch shortly after its origin and, continuing on, forms a broad expansion on one side and then narrowing again it finally terminates in a fusiform thickening. Sometimes a localized thickening of this sort occurs along the course of a process. In Pl. XX, fig. 129 is seen a cell of triangular outline (about 0.015 mm. in diameter), the basal angle of which (on the right in the figure) is produced into a slender process terminating in a broad spatulate expansion with fine vacuoles in its proximal half, its total length being 0.018 mm. In addition, a process tapering into a thin filament arises from the apical angle of the cell. In another cell of similar outline ( $0.018 \times 0.009$  mm. in diameter), a very delicate process reaching the exceptional length of 0.072 mm. is given off from the apical end of the cell, whilst a very short process which splays out fan-wise arises from one basal angle and a short tapering process from the other. We have also encountered cells of quadrangular form presenting a curious superficial resemblance to multipolar nerve cells, inasmuch as one of the four processes arising from the cell is longer and thicker than the others.

We have met with only very few instances in this egg in which anastomotic connections have been formed between the pr. end. cells. Pl. XX, fig. 127 shows a group of three cells, the middle one of which is joined by a vacuolated projection of its body to a corresponding vacuolated outbulging from the cell on the left, whilst the cell below the middle one has given off two processes which have come into contact, if not actual fusion, with the surface of the latter.

The cytoplasm of the pr. end. cells frequently contains one or more large vacuoles, (Pl. XX, fig. 127) and small, mostly rather pale-staining, yolk-spheres are also sometimes present in it.

*Germ-ring*.—The germ-ring, although it reaches a width of up to 0.24 mm. and a thickness of about 0.024 mm., does not present the appearance of being very active. Over about half its width it underlies the margin of the blastoderm, and in this infra-marginal portion the majority of its nuclei, mostly small, finely granular and rather light-staining, are situated.

The peripheral cells of the blastoderm are small and attenuated, and are connected with the flat surface of the germ-ring by thin extensions of their cell-bodies.

The succeeding three eggs, VVH 8, 3, and 28 are in very much the same stage of development. In all three the blastoderm has made decided progress in its growth over the yolk-mass of the egg, only about one-third or less of its surface remaining exposed over the lower polar region. All three are characterized by a considerable decrease in the number of intercalated pr. end. cells and by a marked increase in the number of deep cells. This increase is due partly to the continued emigration of the intercalated cells, partly and indeed mainly to the active mitotic division of the cells, both intercalated and deep. The formation of pseudopodial processes by the deep cells is in active progress, as also is the establishment of anastomotic connections between them. The degree of development of both varies somewhat in the three eggs and has suggested the above seriation, VVH 28 being, if anything, the most advanced of the three in these respects, though it possesses an uncovered lower polar area rather more extensive than those of the other two.

VVH 8. (Pl. XX, figs. 130, 132; Pl. XXI, figs. 131, 133.)

(Diameter of egg, 5.0 mm. (fresh), 5.61 mm (after fixation). Diameter of ovum,  $4.44 \times 4.31$  mm. Circumferential width of blastoderm, about 9.3 mm. (average), and of elliptical lower polar area, about 3.27 mm. (average). Fixation, FBA.)

This egg \* is well in advance of *Echidna* IV. The extent of the blastoderm is much greater than in the latter (9.3 mm. compared with 5.5 mm.); the primitive endoderm cells are more numerous, many more of them have acquired their definitive deep position and now possess well-marked pseudopodial processes.

The blastoderm has now attained a circumferential width of about 9.3 mm., whilst the uncovered lower polar area, elliptical in outline, has become reduced to an average width of about 3.2 mm. (in the intact egg the latter area measured  $3.69 \times 2.86$  mm. in diameter). The total circumferential extent of this egg (based on tangential measurements of the sections) is therefore about 12.5 mm. This compares with a calculated circumferential extent of 13.1 mm. (the egg having an average diameter in the sections, inclusive of the zona-albumen layer, of 4.2 mm.).

*Pros. ect. cells*.—These cells in the superficial layer of the blastoderm (Pl. XX, fig. 130; Pl. XXI, fig. 131) essentially resemble those of *Echidna* IV, but the average diameter of their nuclei is slightly greater, that of 18 in section being  $0.013 \times 0.005$  mm. and in surface view  $0.013 \times 0.012$  mm. Mitotic activity in the

\* In the right uterus, from which this egg was taken, there was also present a second egg, 3.0 mm. in diameter (fresh) and abnormal.



pros. ect. cells is now very pronounced (Pl. XX, fig. 132, *sc.*). In 74 sections some 47 cells were observed to be in division. They are to be found quite close to the germ-ring, and in one instance a peripheral cell was observed in the metaphase.

The peripheral cells are normal in appearance and not enlarged.

*Pr. end. cells.*—These cells (Pl. XX, figs. 130, 132; Pl. XXI, figs. 131, 133, *pr.end.*), in the interval between this stage and *Echidna* IV, have greatly increased in number as the result of intensive mitotic division, and large numbers of them have now migrated to their definitive position below the superficial layer, whilst others are still in progress of migration (Pl. XXI, fig. 131). They are distributed over the extent of the blastoderm, with the exception of a very narrow marginal zone adjoining the germ-ring where, over a width varying from about 0.5 to 2.0 mm., they are absent or only sporadically present.

One specially noteworthy feature in the distribution of these cells in this blastoderm is that they exhibit a marked tendency to occur clumped together in groups. Without making an exhaustive count and leaving aside pairs of cells which are common, we have noted nine groups of three cells, eight of four, six of five, three of six to eight, one of 15, and two of 20 or more. These groups mark foci of more or less intensive mitotic activity, and in some of them cells in division may still be encountered. Moreover, throughout the blastoderm, isolated cells in division, both intercalated and deep, are present in considerable numbers. In 74 sections we have noted 37 *pr. end.* cells in the earlier phases of mitosis, and in addition some 18 pairs of sister-cells in the late telophase (Pl. XXI, fig. 131, *sc.*) as well as 13 spheroidal cells in the same phase which we have not paired up.

These data bear witness to the very considerable additions which have been, and are being made, to the sum-total of *pr. end.* cells present in this blastoderm.

The cells (Pl. XX, figs. 130, 132) are slightly larger than those of *Echidna* IV, the average diameter in 40 measured being  $0.018 \times 0.0099$  mm., and that of their nuclei  $0.010 \times 0.0078$  mm. In their structural characters they differ in no important respect from those of that stage, but in other ways they have made progress. More of them, as stated above, have acquired the deep position, whilst pseudopodial processes, both in intercalated and deep cells, are better developed than in *Echidna* IV (Pl. XX, fig. 132; Pl. XXI, fig. 133). Moreover, there are indications in the tangential sections that the deep cells are beginning to be linked up by the formation of anastomotic connections between the processes of adjacent cells or by the fusion of the process of one cell with the cell-body of another (Pl. XXI, fig. 133, cells 2 and 5). The pseudopodial processes, when they first appear, have often the form of prickle-like projections (Pl. XX, fig. 132, cell on the right, Pl. XXI, fig. 133, cell 1); when more developed they may be long and slender (Pl. XXI, fig. 133, cell 3) or broad and flattened and of variable length (Pl. XXI, fig. 133, cell 4; Pl. XX, fig. 132, cell on the right, where the main process ends in a terminal expansion).

*Germ-ring.*—The germ-ring has a width of about 0.15 mm. (exceptionally 0.19 mm.) and varies in maximum thickness from about 0.018 to 0.027 mm. The peripheral cells of the blastoderm are attached to its surface about 0.075 mm. from its inner margin, the surface-groove being very shallow or absent. Its nuclei usually occur singly in the sections and vary in diameter up to  $0.022 \times 0.015$  mm.

*Yolk-bed nuclei.*—These appear to be absent.

## VVH 3. (Pl. XXI, fig. 134.)

(Diameter of egg, 4.3 mm. (fresh),  $5.76 \times 5.30$  mm. (after fixation). Diameter of ovum,  $4.31 \times 4.26$  mm. Circumferential width of blastoderm, about 9.5 mm., and of lower polar area, about 2.0 mm. Fixation, FBA.)

Apart from a slight increase in the surface-area of the blastoderm, the only significant advance on VVH 8 observable in the sections of this egg is in the richer development of pseudopodial processes by the pr. end. cells and the more frequent occurrence of anastomotic connections between them.

The pros. ect. cells of the superficial layer are of the usual type. Their nuclei are much of the same size as those of VVH 8, the average diameter in 18 measured being  $0.0127 \times 0.0055$  mm. In the marginal region occasional cells enclosing small yolk-spheres are met with.

The pr. end. cells are less numerous than in VVH 8, and a good many of them are still intercalated in the superficial layer. They are well dispersed throughout the blastoderm, mostly singly or in twos, more rarely in groups of three, but as in VVH 8, they are sparse or absent in a narrow marginal zone adjoining the germ-ring. Large groups, such as occur in the latter, are not present.

Measurements show that the cells and their nuclei are fairly comparable in size with those of VVH 8, the average diameter of the cell-body in 18 measured being  $0.0165 \times 0.0098$  mm., that of their nuclei  $0.0095 \times 0.008$  mm.

The pseudopodial processes of the cells seem to have attained a rather higher degree of development than in VVH 8; they reach a greater length (up to 0.054 mm.) and anastomoses between them are more frequently encountered than in the latter. In Pl. XXI, fig. 134, four pr. end. cells (1-4) are seen, forming an irregular row. The oval cell (1) on the left gives off from its tapering end a short slender process directed upwards, and a second, also slender, directed outwards to the margin of the figure, beyond which it continues on to form an anastomosis with a very long process (over 0.054 mm. in length) given off from a cell situated well to the left of cell (1) and not included in the figure. At its opposite end, cell (1) is connected by a broad lightly stained process with the cubical cell (2). This in its turn is connected with the oval cell (3) by a thin strand (0.018 mm. in length) which appears to have been formed by the anastomosis of a shorter tapering process from cell (2) with a longer process from cell (3). In addition, the latter is produced on its right into a short thick process underlying an ectodermal nucleus. Cell (4) on the right contains a few basophil yolk-spheres and is produced above into a short pointed process, and below into a more elongated thick process, slightly expanded and vacuolated at its lower end.

Bipolar cells of the type of cell (4) with a process arising from each end of the cell-body are not uncommon. In one case, one of the processes is very thin and attains a length of 0.030 mm., the other is thicker, 0.016 mm. in length, and terminates in a slight expansion from which two fine filaments are given off.

Mitotic activity, both in the pr. end. and pros. ect. cells, is less in evidence than in VVH 8.

*Germ-ring.*—The germ-ring is well developed. It varies in width from about 0.18 to 0.21 mm. and in thickness, at the level of the nuclei, from 0.018 to 0.024 mm. Over about half its width, it underlies the periphery of the



blastoderm. Its surface is practically flat, and its nuclei mostly occur singly in the sections and attain a diameter of up to  $0.021 \times 0.017$  mm.

*Yolk-bed.*—The yolk-bed and latebra of this egg are figured on Pl. XXI, fig. 117 of Part IV and briefly described on p. 495.

VVH 28. (Pl. XXI, figs. 135, 136, 139, 140, 141; Pl. XXII, figs. 137, 138, 142–145.)

(Diameter of egg, 4.5 mm. (fresh), 5.18 mm. (after fixation). Diameter of ovum, 4.41 mm. Circumferential width of blastoderm, about 8.4 mm. and of the uncovered lower polar area, about 3.4 mm.)

This egg, as the measurements show, is slightly larger than VVH 3, but the blastoderm is of smaller circumferential extent (8.4 mm. as compared with 9.5 mm.) and the uncovered lower polar area of greater extent (3.4 mm. as compared with 2.0 mm.) than in that egg.

The measurements of the blastoderm suggest that the egg is earlier than VVH 8 and 3, but examination of the sections indicates that the pseudopodial processes of the pr. end. cells, and in lesser degree the anastomotic connections between them, are rather better developed than in these stages.

The prospective ectodermal cells of the superficial layer (Pl. XXI, fig. 135) have the normal structure. The average diameter of 18 nuclei measured in section is  $0.0120 \times 0.0059$  mm. and in surface view  $0.0127 \times 0.0113$  mm. Without making an exhaustive count, we have noted in 90 sections some 45 cells in mitosis, a number rather less than observed in VVH 8.

Primitive endoderm cells are present in greater numbers than in VVH 3 and, like those of VVH 8, exhibit a decided tendency to occur in groups. Groups of up to five or six cells are not uncommon, but the very large groups seen in VVH 8 do not occur. The largest group we have encountered comprises 13 cells situated in three consecutive sections. One of the cells is in mitosis, the plane of division being oblique to the surface. A group of six cells, two of them intercalated, is shown in Pl. XXI, fig. 136, and a group of the same number in surface view in Pl. XXII, fig. 143. Although many cells are still wholly or partially intercalated (Pl. XXI, figs. 136 & 139, *pr.end.*), many more of them have acquired their definitive deep position or are in process of so doing (Pl. XXII, fig. 137; Pl. XXI, fig. 140). In Pl. XXI, fig. 140 is shown an exceptionally large intercalated cell (*pr. end.*), the body of which is produced into a tapering, vacuolated process (*pr.*) underlying the adjoining pros. ect. cell, whilst in Pl. XXI, fig. 139 (*pr.end.*) there is present a partially intercalated cell in the late anaphase, the plane of division being oblique to the surface.

In their dimensions the cells are a little larger than those of VVH 8 and 3, the average diameter of 40 measured in section being  $0.019 \times 0.011$  mm. and that of their nuclei  $0.010 \times 0.0088$  mm., whilst in surface view the average diameter of 20 cells is  $0.020 \times 0.014$  mm., that of their nuclei  $0.010 \times 0.0096$  mm. Cytologically the cells are similar to those of preceding stages, except that the cytoplasm in many of them is much more vacuolated (Pl. XXII, figs. 142, 143, 144).

Cells in mitosis (Pl. XXII, fig. 138; Pl. XXI, fig. 139) and pairs of sister-cells in the late telophase or with recently reconstituted nuclei (Pl. XXI, fig. 136; Pl. XXII, fig. 138, *sc.*) are of frequent occurrence. In quite a number of instances we have observed the mitotic figure situated in a clear central area of the cytoplasm

with a fairly definite boundary strongly suggestive at first sight of a persisting nuclear membrane (Pl. XXI, fig. 141, of a pros. ect. cell), but which, as Dr. R. J. Ludford has pointed out to us, is only the rather sharply defined junctional line between the dense granular peripheral cytoplasm and its more fluid non-granular central portion which marks the site of the nucleus and which has been termed by Wassermann \* the "Mixoplasma," and by von Mollendorf † the "Teilungsraum."

The varied form and relations of the pr. end. cells as seen in surface view are illustrated in the series of figures in Pl. XXII, figs. 142-145, taken from the tangential sections. Inspection of these figures shows that the great majority of the cells depicted therein are provided with one or more pseudopodial processes and that anastomotic connections between them, though not yet very numerous, are beginning to be formed (Pl. XXII, figs. 143 & 144).

The cells and their processes exhibit a comparable variety in form to those of VVH 8 and 3. Cells of an irregularly quadrangular shape with two or more of the angles produced into longer or shorter processes are fairly common (Pl. XXII, figs. 143 & 144), as also are oval or fusiform cells of the bipolar type, with two processes arising from opposite ends of the cell-body and often reaching a considerable length. Two such cells are seen in Pl. XXII, fig. 142. Here the bipolar cell on the left possesses one long process, which extends for a distance of 0.018 mm. before it is broken off, and a second thicker process broken off close to its origin, whilst to the right of this cell is a similar but larger cell which has given origin at its upper end to a stout tapering process which reaches the considerable length of 0.042 mm., and also to a slender process (again broken off) from its opposite end. In another cell of this type, the longer of its two processes attained a length of 0.039 mm. Other cells, of very varied shape, are seen in the figures to possess relatively short but quite broad processes which may be tapering and sharp-pointed or truncate (Pl. XXII, fig. 144). In one such cell the oval cell-body, pointed at one end, is prolonged at its opposite end into a short, broad and very granular, fan-shaped expansion, with an irregularly lobed margin 0.023 mm. in width, the maximum width of the cell-body being 0.009 mm.

Anastomotic connections between the cells may be formed by the meeting and fusion of two processes from adjacent cells of approximately equal length, as in Pl. XXII, fig. 145, where the fusion is possibly not quite complete, or a long process from one cell may meet and fuse with the shorter process from another cell. This is apparently about to happen in the case of the two lowermost cells (c.4 and c.5) in Pl. XXII, fig. 144. Or again a short process of one cell may fuse directly with the cell-body of another, as frequently happens when the cells are aggregated in groups (Pl. XXII, figs. 143 & 144). In this case, when the cells move apart, the short cytoplasmic bridges doubtless become drawn out to form thin anastomotic strands of the type seen in section in Pl. XXI, fig. 135 (*pr.end.*). We have observed one exceptional case in which two pr. end. cells are in broad continuity with each other, but it is not possible to say whether this condition is the result of secondary fusion or to failure in the completion of the division of a mother-cell, though we may mention that we have occasionally encountered binucleate pr. end. cells in this and other eggs.

\* *Handb. d. mikr. Anat.* (1929, I, 2).

† 'Der Mechanismus der Mitose, usw.' *Jahreskurse f. ärzt. Fortbildung*, Januarheft, 1938.



*Degenerate cells.*—Deep cells (presumably primitive endoderm cells) in a more or less advanced state of degeneration are fairly numerous and are to be seen in a number of the figures (Pl. XXI, figs. 136 & 139; Pl. XXII, fig. 137, *dgc.*). They vary in shape but are mostly spheroidal or elliptical, and they also vary in size, ranging in diameter up to  $0.016 \times 0.015$  mm., but are mostly smaller than this. In a few instances they attain the size of giant cells (one such measuring  $0.031 \times 0.012$  mm. in diameter, its nucleus  $0.018 \times 0.012$  mm.). The cytoplasm is eosinophil, and may be homogeneous (Pl. XXI, fig. 136) or granular and more or less vacuolated (Pl. XXII, fig. 137). The nucleus may be absent (Pl. XXI, fig. 136) or, when present, small and crowded with basophil granules (Pl. XXI, fig. 139) or pycnotic (Pl. XXII, fig. 137).

*Yolk-bed nuclei.*—These nuclei, curiously enough, reappear here for the first time in this Group. They lie in the peripheral part of the yolk-bed, for the most part close below its surface, though one or two are more deeply situated. They number about 18, of which ten occur in a group in two adjoining sections. They stain rather lightly with eosin and vary in diameter from  $0.007$  to  $0.030 \times 0.027$  mm.

*Germ-ring.*—The germ-ring is very similar to that of VVH 3. It has a total width of about  $0.16$  to  $0.19$  mm., of which about one-third underlies the margin of the blastoderm, and a maximum thickness, varying in the individual sections, of from about  $0.015$  to  $0.024$  mm. Its outer portion consists of a thin superficial zone of denser cytoplasm which thickens to contain the nuclei and a deep vacuolated zone enclosing yolk-spheres, whilst its inner portion is composed, except close to the nuclei, of a delicate cytoplasmic reticulum, also enclosing yolk-spheres. Its nuclei measure up to  $0.021 \times 0.015$  mm. in diameter and mostly occur singly in the sections. The peripheral cells of the superficial layer of the blastoderm are attached to its surface which is practically flat.

VVH 11. (Pl. XXII, fig. 146; Pl. XXIII, figs. 147–152.)

(Diameter of egg,  $4.75$  mm. (fresh). Diameter of ovum,  $4.9 \times 4.48$  mm. (ovoidal). Circumferential width of blastoderm, about  $11.30$  mm. Diameter of uncovered lower polar area,  $0.56 \times 0.43$  mm. Fixation, FBA.)

This egg shows striking progress on the three preceding eggs in two important respects: (a) in the enclosure of the yolk-mass by the spreading blastoderm, and (b) in the establishment of anastomotic connections between the deep pr. end. cells.

The uncovered lower polar area has now become reduced to a minute oval spot, still encircled by the germ-ring and measuring only about  $0.56 \times 0.43$  mm. in diameter. It is seen in sectional view in Pl. XXIII, fig. 151 (*lpa.*).

The circumferential width of the blastoderm (measured in the sections) is approximately  $11.30$  mm. This figure, plus the shorter diameter of the lower polar area, gives a total of  $11.73$  mm. as the circumferential extent of the egg in section, which compares with a calculated extent of  $12.5$  mm., the diameter of the egg in section, including the zona-albumen layer, being  $4$  mm.

The prospective ectodermal cells of the superficial layer have the usual structure (Pl. XXII, fig. 146). Their nuclei show no significant alteration in size, the average diameter of 18 measured in section being  $0.013 \times 0.0045$  mm. and that of 18 in surface view  $0.013 \times 0.012$  mm. Mitotic activity is not very marked; in 50 sections some 23 cells were observed to be in division.

Primitive endoderm cells are present in considerable numbers over the extent of the upper hemisphere of the blastoderm, but over its remainder they are less numerous, and indeed over a width of 1.5 to 2 mm. at its periphery are only occasionally met with, though we have observed a group of six cells (some of them enclosing small eosinophil yolk-spheres) overlying the upper (proximal) half of the germ-ring and immediately adjoining the attachment of the blastoderm to the latter.

The majority of the cells are now deep (Pl. XXII, fig. 146, *pr.end.*), and quite a number of those still intercalated are in process of migration, as evidenced by the fact that a portion of the cell-body or a process of the same underlies an adjoining ectodermal cell.

The cells occur singly, in pairs and occasionally in small groups of 3-8 (Pl. XXIII, fig. 147); in one instance the group comprised about 20 cells and extended through five consecutive sections. They show no significant alteration in their dimensions as compared with those of VVH 28; the average diameter of 30 cells measured in section is  $0.0173 \times 0.0097$  mm. and that of their nuclei  $0.0096 \times 0.008$  mm., whilst that of 20 cells in surface view is  $0.019 \times 0.013$  mm. and that of their nuclei  $0.010 \times 0.009$  mm. Mitotic activity is still quite marked. In 50 sections, 29 cells were noted as being in mitosis, together with four pairs of sister-cells in the telophase. A few binucleate cells were observed, the largest one measuring  $0.036 \times 0.033$  mm. in diameter, nucleus 0.012 mm. Such cells are probably destined to degenerate.

In this egg the cells are more richly provided with pseudopodial processes, and anastomotic connections between them are better developed and more numerous than in the preceding stages (Pl. XXIII, figs. 148, 149, 150). Here and there in the tangential sections, cells, more or less loosely arranged in groups, are met with in which the cells are so connected by anastomoses as to present the appearance of a network (Pl. XXIII, figs. 148 & 150), quite comparable with that figured by one of us (Hill, 1910, Pl. 7, fig. 68) for the primitive endoderm cells of *Dasyurus*. The formation of such cellular networks marks an important advance, heralding as it does the commencing establishment of the definitive endoderm as a continuous sheet of cells. In both the above-mentioned figures, as well as in Pl. XXIII, fig. 147, some of the cells are seen to be in direct contact with each other. Should this condition persist, as it seems to do, such cells can become directly incorporated in the endoderm as plate-like groups.

As we have indicated above, anastomotic connections may be first established when the cells lie close together as in Pl. XXIII, fig. 147, and may subsequently become lengthened and attenuated when the cells move apart, as in the case of the slender connection between the two cells on the left in Pl. XXIII, fig. 150; and in the same way, connections established by the fusion of longer processes with each other or directly with the body of another cell may become lengthened and much reduced in thickness, as seems to have happened in the case of the connection (0.030 mm. in length) between the two cells seen in Pl. XXIII, fig. 149. Here the thicker process of the cell on the left is continuous with the extremely thin thread-like process of the cell on the right, which has evidently been drawn out and secondarily reduced in thickness. A good many cells, especially those of spheroidal form (Pl. XXIII, fig. 147), are still devoid of processes.



Degenerate deep cells, varying greatly in size, are not uncommon. One large cell ( $0.033 \times 0.024$  mm. in diameter) crowded with eosinophil yolk-spheres is still intercalated.

*Yolk-bed nuclei*.—Eleven of these nuclei have been observed, of which eight lie in a finely granular mass of cytoplasm, situated immediately below the surface of the yolk-bed, just outside its central vacuolated zone. Another nucleus lies superficially, in the latter, almost directly above the junction of the bed with the latebral neck.

*Germ-ring*.—The germ-ring (Pl. XXIII, figs. 151 & 152) exhibits no essential change in its structure or dimensions as compared with that in the preceding stages. It varies in width from about 0.15 to 0.22 mm. and in maximum thickness from about 0.018 to 0.027 mm. When traced downwards (peripherally) from the line of attachment of the blastoderm-margin to its surface, it is seen to become gradually reduced in thickness in normal fashion, but instead of fading out completely it seems to pass into continuity with an extremely attenuated net-like layer of cytoplasm enclosing small yolk-spheres, which underlies and is fused with the egg-membrane investing the uncovered lower polar area (Pl. XXIII, fig. 151, *lpa.*). This layer is no doubt the remains of the peripheral cytoplasmic zone of the ovum to which we have previously made reference (*ante*, p. 47).

The germ-ring itself (Pl. XXIII, fig. 152, *gr.*) consists of a superficial zone of eosinophil yolk-free cytoplasm which reaches its maximum thickness around the nuclei and is vacuolated in its upper (proximal) half and more compact in its tapering lower (distal) half and of a deep zone in the form of a delicate network, enclosing yolk-spheres. Its nuclei are eosinophil, active-looking and large, their diameter ranging from  $0.015 \times 0.008$  mm. to  $0.024 \times 0.014$  mm. Its surface is flat and the peripheral cells of the superficial layer of the blastoderm are attached to its mid-region, directly above the nuclei, its proximal half being infra-marginal (Pl. XXIII, fig. 152, *bl.*).

#### *Echidna* I. (Pl. XXIV, figs. 153–161.)

(Diameter of egg, 4.0 mm. (fresh),  $5.5 \times 5.4$  mm. (in alcohol). Diameter of ovum,  $4.16 \times 4.04$  mm. Fixation, FBA.)

This is the last and most advanced of the *Echidna* eggs available for inclusion in Group V. It constitutes a most interesting and important stage, inasmuch as the blastoderm has now made quite definite and unmistakable progress towards the attainment of the bilaminar condition.

Unfortunately the serial sections of the egg comprise only the upper hemisphere, so that it is not possible to describe the condition of the blastoderm over the lower polar area; but examination of the intact ovum (as recorded in our original notes) revealed the presence at the lower pole of a small slightly elliptical area  $1.20 \times 1.09$  mm. in diameter, bounded by a narrow marginal zone, whitish-looking and opaque, and wider on one side than on the other. Situated centrally in this area there was present a disc-like patch, about 0.30 mm. in diameter, surrounded by a more transparent ring-shaped zone. This patch is almost certainly the yolk-navel. It is fairly comparable in size with the navels of the two early primitive streak stages of *Echidna*, described below (pp. 94–96).

The blastoderm varies considerably in thickness from place to place, depending on its constitution. Where it is composed of the superficial layer alone it may have a thickness of as little as 0.0035 mm., but where it is two cells thick it may reach 0.010 mm. or even more.

*Superficial layer.*—It is still not possible to speak of the superficial layer as the ectoderm, since small numbers of pr. end. cells are still intercalated in it. The ectodermal cells (Pl. XXIV, figs. 153–155, *ect.*) have the same flattened spindle-shaped form as in the preceding stages and, except where interrupted by still intercalated pr. end. cells, form a continuous layer. The average diameter of 47 of their nuclei measured in section is  $0.011 \times 0.0057$  mm., and that of 18 in surface view  $0.011 \times 0.010$  mm. They are thus definitely smaller than those of VVH 11, a decrease indicative perhaps of some increase in the number and a reduction in the size of the cells in this stage. Mitotic activity is considerable.

*Endoderm.*—Though numbers of primitive endoderm cells still occur intercalated in the superficial layer, singly, in twos or in small groups of three, four or more cells (Pl. XXIV, fig. 156, *pr.end.*), the great majority have acquired their deep position and have assumed the form in section of more or less flattened fusiform elements which tend to be closely applied to the deep surfaces of the ectodermal cells (Pl. XXIV, figs. 153, 156, 157, *end.*). But occasional spheroidal and ovoidal cells are still to be met with, and a few spheroidal cells have migrated in the wrong direction and have come to lie between the blastoderm and the zona-albumen layer.

As yet, the endoderm is far from being a complete or connected layer, for there are areas in the sections where deep cells are absent, the blastoderm consisting of the superficial layer alone, and other areas where scattered deep cells, apparently isolated, occur below it (Pl. XXIV, fig. 153). Such cells are mostly fusiform, but here and there spheroidal, ellipsoidal or oval cells are still to be found. On the other hand, there is ample evidence in the sections of the occurrence of small areas comprising up to four, five or more cells with their fusiform bodies in direct continuity with each other and where, accordingly, the blastoderm is genuinely bilaminar (Pl. XXIV, figs. 154 & 157).

In the tangential sections, cells are occasionally encountered with their margins in contiguity, others are seen to be joined together by anastomotic bridges such as we have figured in preceding stages, and yet others of very varying form are to be observed provided with one or more cytoplasmic processes as well as sparse spheroidal cells devoid of such.

The evidence clearly shows that the definitive endoderm is now in process of taking form, though it is still far removed from the condition of a continuous cell-membrane, being represented by small areas of flattened cells so connected by their processes as to form irregular cell-networks, by small sheet-like groups of cells in contact by their margins, and by scattered cells with or without processes, still unconnected with each other and irregularly distributed between the cell-networks and cell-sheets.

Cytologically the cells differ in no essential respect from those of the preceding stages. In size they approximate closely to those of VVH 11. The average diameter of 24 cells in section is  $0.0169 \times 0.008$  mm. and that of 38 nuclei  $0.010 \times 0.0065$  mm., whilst the average diameter of 34 nuclei in surface view is  $0.010 \times 0.008$  mm. The slight reduction in the average sectional thickness of



the nuclei in this egg, as compared with VVH 11, is to be correlated with the greater abundance of cells of the flattened fusiform type.

Mitoses are fairly common both in intercalated and deep cells (Pl. XXIV, fig. 157). One intercalated cell was observed with the plane of division parallel to the surface, and a second with the plane of division slightly oblique thereto (Pl. XXIV, fig. 158). This figure also illustrates a not uncommon feature in the metaphase in *Echidna* cells, and that is the delayed completion of the splitting process in one or more of the chromosomes, the two daughter-chromosomes remaining for a time connected by their tips. In Pl. XXIV, fig. 157, the pr. end. cell in the prophase shown therein, is still partially intercalated, though the endoderm has been completed below it,

A few groups comprising up to seven or eight mostly large, rounded or oval pr. end. cells have been noted.

One very interesting phenomenon in connection with the endoderm in this stage remains to be mentioned, and that is the commencing enclosure by the cells of large basophil yolk-spheres. As recorded in the descriptions of preceding stages, pros. ect. and more rarely pr. end. cells, in the peripheral region of the blastoderm especially, are quite frequently seen with small yolk-spheres enclosed in vacuoles in their cytoplasm; and even in this stage, sparse pr. end. cells are still to be found enclosing small eosinophil spheres. But now a quite new phase in yolk-absorption has set in, inasmuch as many of the endodermal cells in the peripheral region of the blastoderm, outside its upper polar region marked by the yolk-bed, are in active process of enclosing large basophil yolk-spheres.

The fact that the endoderm of the Monotreme is a genuine "yolk-endoderm," composed of large, usually plate-like cells, laden with large yolk-spheres of varying diameter and attaining its maximum development in the extra-embryonal region, is well known (Semon, 1894, Hill and Martin, 1894, Wilson and Hill, 1907). We had long assumed that the large yolk-spheres were taken up secondarily, but just when and how they came to be enclosed in the cells we are only now able to resolve. It turns out to be a very interesting process. It is not effected by simple engulfment as happens in the case of the small spheres. The large spheres are too bulky for that, and so the cells proceed to grow round and envelop them. Enclosure of a yolk-sphere may apparently be effected by a single cell (Pl. XXIV, fig. 157) or, as appears often to be the case, by two cells (Pl. XXIV, fig. 155). In the former case, when a yolk-sphere, liberated by the breaking down of the egg-membrane, comes into contact with a cell, the latter reacts and is incited to active growth. It becomes closely applied to the surface of the sphere or rather to that of its enclosing yolk-mantle, so that its surface of contact appears crescentic when viewed in section (Pl. XXIV, figs. 159 & 160). The thin circular margin of the cell now proceeds to grow over the sphere in the form of an attenuated cytoplasmic mantle, and this, closing in below, effects its complete enclosure (Pl. XXIV, fig. 157).

The process is precisely similar when two cells are involved. The cells are usually found lying on opposite surfaces of the upper half of the sphere, having so orientated themselves as to lie approximately at right angles to the surface of the blastoderm (Pl. XXIV, fig. 155). They grow towards each other and unite over the sphere, and at the same time their cytoplasm extends downwards over it as a very thin layer until envelopment is complete. Although it is

the deep cells that are almost exclusively concerned with this process of enclosure, cells still intercalated also seem able to participate.

The rather frequent occurrence of mitosis in the enveloping cells is a further interesting reaction on their part to the task on hand. We illustrate three examples of such dividing cells. Pl. XXIV, fig. 159 shows a cell (roughly triangular in form and  $0.018 \times 0.012$  mm. in diameter) in the prophase or early metaphase which surmounts and is in process of enclosing a yolk-sphere. In Pl. XXIV, fig. 160 is seen a crescentic cell (about  $0.021 \times 0.007$  mm. in diameter) lying in contact with the yolk-mantle of a sphere and containing a mitotic figure in the metaphase, whilst Pl. XXIV, fig. 161 shows two daughter-cells in the telophase and all but completely separated, closely investing the yolk-mantle of a sphere. Possibly some of the cases in which two cells seem to have been concerned in the enclosure of a sphere are to be explained by the division of a mother-cell in this way.

A small proportion of the spheres in process of enclosure are curiously altered. Instead of being homogeneous and staining uniformly throughout, they may be coarsely granular and light staining (Pl. XXIV, figs. 154 & 157), or they may consist of a hardly staining greyish matrix, with centrally a dense clump of basophil granules and sometimes sparse granules peripherally. Some process of digestion or dissolution seems indicated.

Lastly in this connection, it is deserving of mention that, over the yolk-bed which marks the central region of the future embryonal area of the blastoderm, the yolk- or egg-membrane is largely intact, and the endoderm cells, which in this region mostly appear isolated, show little or no signs of taking up yolk-spheres (Pl. XXIV, fig. 153). In the peripheral region of the blastoderm, although, in some places, the egg-membrane is still intact, in many other places it has broken down, so that the superficially situated yolk-spheres are free to come into direct contact with the endoderm cells (Pl. XXIV, fig. 154).

*Yolk-bed nuclei.*—Such nuclei appear to be absent.

*Platypus* S and SS. (5.9.05). (Pl. XXV, figs. 162–166, *Echidna* XIII, figs. 167 & 168, and *Echidna* XIV, fig. 169.)

This stage, the last to be dealt with in this part of our investigation, marks the culmination of the process of primary germ-layer formation in the Monotremes and comprises two twin-eggs of *Ornithorhynchus*, designated S and SS.

These eggs, collected at the Barrington River, N.S.W. so long ago as 1905, were fixed in micro-nitric acid and prove to be in an excellent state of preservation. The diameter of both eggs is stated in our original notes to be 6 mm. in alcohol. After removal of the shell, the ovum in S measured 4.16 mm. in diameter, and in SS, 4.10 mm.

The shell in egg S has a thickness of about 0.009 mm.

Although twin-eggs, SS is distinctly in advance of S. The latter egg is practically at the same stage of development as the preceding stage, *Echidna* I, whereas in SS, over the major portion of the upper hemisphere, the blastoderm has attained the bilaminar condition (Pl. XXV, figs. 165 & 166).

Unfortunately, in both eggs, the lower hemisphere was removed prior to imbedding and in both the serial sections are very incomplete. Of egg S, some 40 sections only are available for study, and of SS, 55 sections. In both cases, however,



the sections include the yolk-bed and are quite reasonably good, so that it has been possible to determine the main structural features of the upper hemispheres in the two eggs.

*Egg S.*—As in *Echidna I*, the blastoderm varies considerably in its constitution from place to place. Over quite small areas in the sections, it is unilaminar and formed by the superficial layer alone, over still larger areas it consists of the superficial layer with scattered endoderm cells below it, whilst over other stretches it is bilaminar and formed of a superficial layer of spindle-shaped ectodermal cells and a deep layer of mostly flattened endoderm cells, all of which conditions may be encountered within the limits of one and the same section (Pl. XXV, figs. 162, 163, 164). The bilaminar areas, which are in all respects similar to those of egg SS, are, curiously enough, more extensively developed on one side of the yolk-bed than on the other, where many of the endoderm cells still appear to be isolated, though groups composed of two to four cells connected together are quite common (Pl. XXV, fig. 164) and are clearly on the way to becoming organized into a continuous cell-membrane.

The ectodermal cells of the superficial layer have the usual flattened spindle-shaped form and possess oval, flattened, light-staining nuclei, with an average diameter in 18 measured of  $0.010 \times 0.0045$  mm., the range in diameter being from  $0.009 \times 0.003$  mm. to  $0.012 \times 0.006$  mm. Cells in mitosis are present in fair numbers.

The endoderm cells when connected are mostly fusiform and more or less flattened; when free and isolated (Pl. XXV, fig. 163) they may be fusiform, oval, elliptical or more rarely spheroidal.

The three latter types of cells conform in their characters to primitive endoderm cells. Their cytoplasm is rich in basophil granules, occasionally exhibits slight vacuolation and, like the nucleus, stains rather deeply. The nucleus, oval or elliptical, is large relatively to the cell-body. The average diameter of 18 nuclei measured is  $0.009 \times 0.006$  mm., the range in diameter being from  $0.007 \times 0.006$  mm. to  $0.010 \times 0.0067$  mm. They are thus slightly smaller but less flattened than the ectodermal nuclei.

Primitive endoderm cells still occur intercalated in the superficial layer, but only in small numbers. They mostly occur singly but occasionally in small groups of up to three cells, rarely more. In Pl. XXV, fig. 163 (*end.*) on the right, there are present two fusiform endoderm cells, intercalated and partially overlapped by the adjacent ectodermal cells, but here they are connected by a thin cytoplasmic strand passing below the intervening ectodermal cell, a somewhat exceptional condition, though it is not unusual to find intercalated cells provided with one or two cytoplasmic processes.

Small basophil and eosinophil yolk-spheres are present in some of the deep endoderm cells, but neither in this egg nor in SS is there as yet any concerted attempt on the part of the latter to enclose large yolk-spheres, a curious time-lag as compared with *Echidna I*.

*Egg SS.*—As mentioned above, the blastoderm of this egg over the greater part of the upper hemisphere, which alone is available for study, has attained the bilaminar condition, though there are still present small isolated areas where the endoderm has not yet become established as a continuous membrane.

Pl. XXV, figs. 165 & 166 illustrate the condition prevailing over the central region of the yolk-bed and peripherally thereto, eight ( $10\mu$ ) sections separating the two figured. They demonstrate that the fully-established blastoderm consists of a thin superficial layer composed of large flattened ectodermal cells and an underlying layer of correspondingly flattened endodermal cells, and it can be stated that this condition prevails over the major portion of the upper hemisphere preserved in the sections.

The figures also demonstrate that the blastoderm is now separated from the yolk-bed by a well-marked space (*sgc.*) which varies somewhat in depth, attaining a maximum of about 0.04 mm. a little to one side of the centre of the yolk-bed, and a maximum width of about 0.54 mm. We regard this space as the belated representative of the sub-germinal cavity of the Sauropsidan egg. Besides a small number of dispersed yolk-spheres, it contains traces of a delicate, finely granular coagulum, and was doubtless fluid-filled during life. In addition, there is present in it, adjacent to the surface of the yolk-bed, a considerable number (about 24) of free oval or spheroidal endoderm cells, some of them enclosing small eosinophil yolk-spheres. Eleven of them form a loose group extending through five sections (Pl. XXV, fig. 165), the remainder occur in smaller groups or singly. Intermingled with them are a few large basophil yolk-spheres. These cells are doubtless destined to degenerate. In egg S, a small plano-convex space overlies the vacuolated central area of the yolk-bed, but whether this is an artifact or marks the beginning of the sub-germinal cavity cannot be determined with certainty from the available sections. The appearances rather suggest the former alternative, since the space seems to have arisen through a localized breakdown of the superficial vacuoles in the yolk-bed, and such a mode of origin of the sub-germinal cavity is hardly in consonance with the smooth even character of its floor in egg SS (Pl. XXV, fig. 165).

The structure of the bilaminar blastoderm is illustrated in Pl. XXV, figs. 165 & 166 (already referred to above). The ectoderm (*ect.*) is composed of large, mostly flattened, spindle-shaped cells with flattened, oval, light staining nuclei. The average diameter in 18 nuclei measured is  $0.011 \times 0.005$  mm., the range in diameter being from  $0.009 \times 0.004$  mm. to  $0.013 \times 0.005$  mm. The cells of the endoderm (*end.*) are slightly more variable in their form than those of the ectoderm. The great majority are again flattened and spindle-shaped with oval nuclei slightly smaller than the ectodermal, the average diameter in 18 measured being  $0.009 \times 0.005$  mm., the range in diameter being from  $0.006 \times 0.004$  mm. to  $0.012 \times 0.007$  mm. But intercalated amongst the flattened cells, plump oval and fusiform cells are met with in small numbers and more rarely spheroidal cells with dark staining granular cytoplasm. Such cells also occur isolated below the ectoderm where the endoderm is still incomplete and occasionally occur below the endoderm itself.

A few primitive endoderm cells are still to be found intercalated in the ectoderm. They mostly occur singly in places where the endoderm has not yet been completed and occasionally are to be seen in mitosis.

Degenerate spherical and ellipsoidal cells occur in small numbers below the blastoderm.

*Yolk-navel.*—We think it highly probable that here also, as in *Echidna* I, the yolk-navel has been established by the final closing-in of the germ-ring and



blastoderm over the lower polar area, with the result that the yolk-mass of the egg has become completely enclosed in a thin blastodermic membrane.

The developmental importance of this complete enclosure of the yolk-mass lies in the fact that the egg is thereby converted into a potential vesicle or blastocyst, possessed of a continuous cellular wall and so capable of increasing in size. In this way room is provided for the development of the embryo and for absorbing and storing up the nutritive fluid which is secreted by the tubular glands in the uterine wall, and which is necessary for the nutrition of the embryo during the remainder of the intra-uterine period and the whole of the incubatory period of its life-history. This growth and absorptive activity suffices to account for the increase in the diameter of the egg, which is observable in this stage, and it may also account for the appearance of the sub-germinal cavity. In this connection it is deserving of mention that there is evidence of considerable mitotic activity in the cells of both the ectoderm and the endoderm, and of the presence below the blastoderm in both eggs of varying amounts of granular coagulum (Pl. XXV, fig. 162, *cg.*), indicative of the absorption of fluid from the uterine lumen.

Although we are unable, for the reason stated, to describe the condition of the yolk-navel in the present stage, we possess serial sections of a small number of eggs of *Echidna* in early primitive streak stages, in which it is clearly displayed. A brief description of its structure in two of these eggs may be included here, to supplement the foregoing account of *Platypus* SS.

The youngest of the two, *Echidna* XIII, with an egg 5.7 mm. in diameter, possesses a primitive streak primordium measuring only  $\pm 0.6$  mm. in length, and is thus not very greatly in advance of *Platypus* SS. In this egg the endoderm has attained the condition of a continuous membrane, and enclosure of the yolk-mass has been completed with the establishment of the yolk-navel at the lower pole. Its appearance in section is illustrated in Pl. XXV, figs. 167 & 168, the former depicting a section through its centre, the latter a section through its marginal region. From the figures it will be seen that the navel takes the form of a small localized thickening in which there is present centrally a well-marked depression or cavity opening outwards (Pl. XXV, fig. 167, *nc.*). This we may term the navel-cavity. The navel forms a slight projection on the surface and bulges convexly upwards into the overlying yolk. It is approximately circular in outline, having a sectional extent of 0.21 mm. and a maximum width of about 0.24 mm., whilst it measures in thickness about 0.14 mm. It will also be seen that it is formed of two distinct constituents, a superficial cellular part (*ect.m.*) and an overlying, non-cellular, cytoplasmic layer (*gr.c.*), enclosing small yolk-spheres in its peripheral zone which abuts on the yolk. Study of the sections shows that its cellular constituent has been formed by the proliferation of the marginal ectoderm bordering the small area of exposed yolk (navel-area) at the lower pole, and that it takes the form of an irregularly thickened rim or lip surrounding the above-mentioned navel-cavity, whilst its cytoplasmic constituent has been furnished by the germ-ring.

In sections through the periphery of the navel, the thickened rim of marginal ectoderm has been cut tangentially, and in Pl. XXV, fig. 168 (*ect.m.*) appears as a well-defined projecting knob, composed for the most part of large cells and enclosing below its surface an oval space, bounded by a layer of small flattened

cells. In the central sections (Pl. XXV, fig. 167) the thickened ectodermal rim (*ect.m.*) has been cut more or less transversely and appears in the form of two marginal lips, separated by the mentioned navel-cavity. These lips are markedly but asymmetrically thickened, the lip-thickening appearing in the sections first on one side (left in the figure) and then thinning out as the opposite lip thickens up. Peripherally the lips are in definite continuity with the thin blastodermic ectoderm (*ect.*), and they enclose between them the relatively wide navel-cavity, (*nc.*), open below but roofed over above by the cytoplasmic layer, formed by the germ-ring. It should be mentioned that the elongated oval mass of cells seen in Pl. XXV, fig. 167, lying below the navel-cavity and in contact with the zona-albumen layer, is a detached portion of the left lip, now much reduced in the section figured, whilst the right lip is much thickened.

From these relations it is clear that, although the marginal ring of ectoderm round the navel-area has thickened and closed in from all sides below the already continuous layer formed by the germ-ring, closure of the ectoderm has not yet been completely effected, the central navel-cavity still remaining to be occluded.

The remaining (germ-ring) constituent of the navel takes the form of the before-mentioned relatively thick, irregularly saucer-shaped layer of granular cytoplasm (measuring about 0.24 mm. in width and 0.064 mm. in maximum thickness) which overlies the ectodermal constituent and roofs over the navel-cavity (Pl. XXV, fig. 167, *gr.c.*). It contains remarkably few nuclei (the germ-ring nuclei having apparently degenerated and been resorbed, with the exception of two or three) and is finely as well as coarsely vacuolated, vacuolation being most extensive in a narrow peripheral zone on its upper side, in which are enclosed numbers of small yolk-spheres. With the periphery of this layer the endoderm has become loosely connected. That complete closure of the germ-ring should be effected before that of the ectodermal margin is only to be expected in view of its position in advance of the latter.

It would appear that the yolk-navel is subject to some individual variation in the details of its form, quite apart from differences due to age, for in *Echidna* XIV, with an egg 5.4 mm. in diameter and a primitive streak about 1.26 mm. in length, it presents a rather different appearance to that of *Echidna* XIII, though the same two constituents are readily recognizable in it, and it is of much the same size (sectional extent 0.025 mm., width about 0.20 mm., thickness 0.19 mm.). Here, the ectodermal margin of the blastoderm around the navel-area (Pl. XXV, fig. 169, *ect.m.*) has not only thickened but has proliferated inwards to form a short, thick-walled, tubular structure with a cleft-like lumen (the equivalent of the outer part of the navel-cavity in the navel of *Echidna* XIII), which opens at the surface and also at its inner end (Pl. XXV, fig. 169, *nc.l.*). It is thickest at the surface, where it forms a slight projection, and as it continues inwards its central part separates off as a narrow tubular prolongation which projects spout-like into the basin-shaped navel-cavity seen in the figure (*nc.*) and into which the lumen opens. In the cavity, small numbers of spheroidal cells, isolated and in clumps, are present.

Surrounding the mid-region and inner part of the ectodermal tube, and not everywhere sharply marked off from it, is the germ-ring constituent in the form



of an irregular, rather ill-defined collar of cytoplasm, mostly much vacuolated and very poorly delimited on its outer side. It is richer in nuclei than is the corresponding layer in *Echidna* XIII, but the nuclei are small and more or less degenerate. From this collar there extends inwards a thin but well-defined layer which forms a complete boundary to the expanded inner part of the navel-cavity (*nc.*), the layer being composed of a pellicle of dense cytoplasm with sparse yolk-granules, next the latter cavity and an overlying zone of very delicate much vacuolated cytoplasm enclosing sparse fine yolk-spheres (Pl. XXV, fig. 169, *gr.c.*).

The somewhat extensive navel-cavity here present can be assumed to have arisen by the expansion upwards, perhaps as the result of fluid-accumulation, of just such a cavity as is present in the navel of *Echidna* XIII, with concomitant narrowing of its opening and thinning out of the germ-ring cytoplasm.

It may be recalled here that in two primitive streak stages of *Ornithorhynchus*, much later than those of *Echidna* above referred to, Wilson and Hill (1907) described and figured in their specimens DD and Y, two other variants of the yolk-navel (their figs. 9 and 10, Pl. 4 and fig. 11, Pl. 5), though at the time they failed to recognize the structure they described as the yolk-navel and regarded it as the primitive knot, a mistake in interpretation they later corrected (Wilson and Hill, 1915). In the yolk-navel of specimen DD, the navel-cavity (originally regarded as an "archenteric cavity" by these authors) is represented by a curved flattened space, canal-like in section and opening on the surface. Over its outer part it is bounded by an inward continuation of the ectoderm, slightly thickened on one side of the opening, but over its blindly ending inner part its boundary is largely formed by the layer of germ-ring cytoplasm. In specimen Y there is no navel-cavity, but in the position of the cavity (*nc.*) in Pl. XXV, fig. 167 of *Echidna* XIII, there is present a solid cellular plug, evidently derived from the ectodermal margin of the navel-area, here completely closed. In both specimens the germ-ring cytoplasm is markedly developed.

For a comparison of the Reptilian yolk-navel with that of the Monotreme, the reader is referred to pp. 110–111.

*Yolk-bed.*—In egg S the fine-grained region of the yolk-bed has a width of about 0.56 mm. and it is for the most part coarsely vacuolated. Centrally it deepens to form a lighter staining, roughly triangular area (about 0.16 mm. in width and the same in depth), above which lies the space (? sub-germinal cavity) referred to above. Its apex passes into continuity below with the latebral neck. This central area is rich in fine basophil granules and its upper part is coarsely and fairly uniformly vacuolated, in its lower part the vacuoles are fewer in number but larger and rounded. The upper part of the latebral neck presents a striking appearance, owing to the presence in it of a row of mostly quite large rounded vacuoles, a condition we have several times observed in the *Platypus* egg (*cf.* Gatenby and Hill, 1924, text-fig. 1).

In egg SS the yolk-bed (Pl. XXV, fig. 165) is very similar to that of S, except that the vacuolar spaces in the deep part of the central area are much more irregular in form and those in the latebral neck are quite small.

*Appendix to Group V.**Echidna* IX (6.8.31). (Pl. XXVI, figs. 170–172.)

(Diameter of egg,  $5.6 \times 5.56$  mm. (in alcohol). Diameter of ovum,  $4.5 \times 4.16$  mm. Fixation, PNO.)

Although abnormal, this is a very interesting and instructive stage from the point of view of the mode of growth of the blastoderm. The fixation is excellent and the sections are quite reasonably good.

The interest of this egg lies in the fact that the blastoderm, though it has attained a circumferential extent of only about 2.14 mm., and so should be intermediate between VVH 6 of Group III and VVH 32 of Group IV, clearly belongs to Group V, since deep as well as intercalated primitive endoderm cells are present in it in fair numbers (Pl. XXVI, fig. 170, *pr.end.*). In its stage of development it approximates most nearly to *Echidna* IV.

The blastoderm, quite evidently, has been retarded in its peripheral growth, and since all the evidence goes to show that that growth is conditioned by the peripheral migration of the germ-ring, it is clear that some structural or other defect must have adversely affected the migratory capacity of that structure. Examination of the sections reveals, indeed, the existence, at the periphery of the blastoderm, of detached cells, often occurring in groups, which might well be supposed to have had an adverse influence on the migratory activity of the germ-ring. The cells in question directly overlies the junction of the blastoderm with the latter and occupy the space between it and the zona-albumen layer (Pl. XXVI, figs. 171 & 172, *cgp.*). Curiously enough, they are more numerous on the apparent near-side in the sections than on the opposite side, and in this connection it is perhaps deserving of mention that the extent of the blastoderm on the apparent near-side, measured from the centre of the yolk-bed to its junction with the germ-ring, is 0.91 mm., whereas on the opposite side the corresponding measurement is 1.23 mm., a difference of 0.32 mm. But caution, in attaching significance to this difference, is necessary in view of the lack in coincidence between the centre of the blastoderm and that of the yolk-bed which occasionally occurs, and to which we have previously directed attention (*ante*, p. 76).

We are not, however, satisfied that this anomalous condition at the periphery of the blastoderm provides the real explanation of the retardation in the activity of the germ-ring as we at first concluded, and the possibility that it is the result and not the cause of the latter must not be overlooked (*v. infra*).

The pros. ect. cells have the normal structure. They are for the most part fusiform but are not so drawn out as in blastoderms of greater extent. Their nuclei (oval or flattened) are approximately of the same size as those of *Echidna* IV, having an average diameter, in 14 measured, of  $0.010 \times 0.0063$  mm.

The pr. end. cells, both intercalated and deep, are fairly numerous, and a few of the deep cells show indications of cytoplasmic processes. They also agree closely in size with those of *Echidna* IV. The average diameter in 40 cells measured is  $0.017 \times 0.009$  mm. (the cells ranging in diameter from  $0.013 \times 0.007$  to  $0.024 \times 0.010$  mm.), whilst their nuclei average in diameter  $0.008 \times 0.0067$  mm. (the range being from  $0.006 \times 0.0045$  to  $0.009$  mm.). The cells vary in shape but are mostly oval or oblong, rarely spherical. They occur singly, in pairs and small groups,



whilst, curiously enough, considerable numbers of them occur together in and below an extensive area of the blastoderm, situated a little to one side of the central region of the yolk-bed (Pl. XXVI, fig. 170, *pr.end.*, left side). This area may reach a width in the sections of up to 0.14 mm., and it extends through some 30 sections, *i. e.* over a length of about 0.30 mm., though it varies in width and in thickness over its extent. The cells have the usual characters, the cytoplasm being finely granular and staining deeply, as also does the relatively large nucleus.

Mitotic activity is not very marked and appears to be confined to the intercalated cells (Pl. XXVI, fig. 170, *pr.end.*).

*Marginal region and Germ-ring.*—The marginal region of the blastoderm is somewhat variable in its constitution and is rarely more than one cell thick, though deep (sub-marginal) cells to the number of one or two are occasionally present close to its junction with the germ-ring (Pl. XXVI, fig. 171, *smc.*). Its constituent ectodermal cells are mostly thin and fusiform, but towards the actual margin, over a width of several cells, they may be enlarged and oval or oblong in form and may contain small yolk-spheres. The actual peripheral cells also vary considerably in form and size, but are mostly fusiform and only rarely contain yolk-spheres. In a few instances they have the characters of *pr. end.* cells. The connection with the germ-ring is usually effected by a short thin extension of the cell-body which fuses with the surface of the germ-ring, or sometimes with a slight ridge-like elevation of the same.

Pl. XXVI, fig. 171 illustrates a fairly typical section from the apparent near-side, showing the germ-ring, the marginal region of the blastoderm and the above-mentioned detached cells forming a group overlying the junction of the two. The marginal portion of the blastoderm (*mbl.*) is seen in the figure as a thin layer of fusiform cells which passes in between the cell-group and two vacuolated sub-marginal cells (*smc.*), to become attached to the germ-ring, but such sub-marginal cells are not of frequent occurrence.

The germ-ring itself cannot be described as well developed. It is narrow, with a width of about 0.10 to 0.12 mm., of which about half or rather less underlies the margin of the blastoderm and a thickness below the junctional line with the blastoderm, where it attains its maximum, of from 0.018 to 0.021 mm. It consists of the usual cytoplasmic matrix, enclosing yolk-spheres below, but is quite exceptional in containing a small number of large irregular vacuolar spaces, one of which is seen in Pl. XXVI, fig. 171.

Numerous nuclei are present in its thicker region. They vary greatly in size, many of them being so small as to suggest an origin by budding or fragmentation.

We have observed two instances of yolk-laden cells (one of them probably a sub-marginal, the other a detached cell) partially buried in depressions in the germ-ring, and at least three cases of cells which have become completely enclosed in it.

In many of the sections on this apparent near-side, it looks at first sight as if the connection of the blastoderm with the germ-ring had been disrupted by the group of detached cells, the blastoderm apparently terminating in the latter, as seems to be the case in the section illustrated in Pl. XXVI, fig. 172. But it is more probable that the two large cells in that figure which form the direct continuation of the thin blastodermic membrane really belong to the latter, the actual peripheral cell (*pc.*) abutting directly on the germ-ring.

In the section illustrated in Pl. XXVI, fig. 171, the group of cells there present has a width of about 0.066 mm. and a thickness of 0.018 mm., and is formed of nine cells of varying size, compactly arranged. But such groups vary considerably in their dimensions and in some sections attain a width of 0.09 mm. There is also considerable variation in the number of cells composing them. Seven to nine is not unusual, but the number may be reduced to one or two, and there is also much variation in the size and structural characters of the cells themselves. They are mostly oval and vary in diameter from  $0.013 \times 0.010$  mm. to  $0.030 \times 0.020$  mm. Frequently the cells are much vacuolated and more or less rich in fine basophil yolk-spheres, or some of them may be densely crowded with small spheres of fairly uniform size (Pl. XXVI, fig. 172). In addition, small oval or rounded cells with granular cytoplasm, little or no vacuolation and few yolk-spheres or none, are common.

On the apparent far side in the sections, the germ-ring is even more poorly developed than its counterpart on the near-side, being thinner and much less rich in nuclei. Moreover the detached cells overlying the marginal region of the blastoderm are few in number (one to three, rarely more, appearing together in individual sections). They usually occur isolated and are mostly large and yolk-laden. The cells of the marginal region of the blastoderm itself, including the actual peripheral cells, are often enlarged and rich in yolk, and the same holds true for the sub-marginal cells which are not numerous. The peripheral cells mostly appear to be connected with a projecting ridge of the germ-ring by the usual thin extensions of their cell-bodies.

Altogether the sectional appearance of the germ-ring and the adjoining margin of the blastoderm on this apparent far side is in no way suggestive of active growth.

The groups of cells and isolated cells described above have clearly been derived from the marginal region of the blastoderm by proliferation or detachment therefrom, but whether their presence is, so to speak, secondary and the outcome of the failure of the germ-ring to migrate in normal fashion over the yolk, or whether this failure on the part of the germ-ring has been induced by the presence of these cells, as we at first concluded was the case (Flynn and Hill, 1942), is not easy to determine. We now think, however, judging from the structural condition of the germ-ring, that the former alternative is the more probable of the two, and that some inherent defect in the germ-ring itself has largely inhibited its migratory capacity. The detached, as well as the buried, cells at the periphery of the blastoderm in this case could be interpreted as the expression of its thwarted growth-activity. Whether this be the true explanation or not, it is clear that in this egg the normal harmonious relationship between the periphery of the blastoderm and the germ-ring has been seriously disturbed by some abnormal condition affecting one or other of these parts, and we may conclude that failure of the germ-ring to migrate outwards over the yolk-mass of the egg results in a correlated failure of the blastoderm to increase in surface-extent.

*Degenerate cells.*—Numbers of degenerate cells, as well as cells in process of degeneration, are present below the blastoderm.

*Sub-disc nuclei.*—We have observed only one sub-disc nucleus ( $0.024 \times 0.016$  mm. in diameter), situated to one side of the centre of the yolk-bed, close below the yolk-membrane.



*Echidna* TLB 1. (Pl. XXVI, figs. 173 & 174.)

(Diameter of egg, 6 mm. (in alcohol). Shell, about 0.010 mm. in thickness. Fixation, Picro-nitric Acid.)

For this egg we are indebted to the late Dr. T. L. Bancroft, Queensland. It was collected in 1922. Its interest centres in the fact that it harbours in its zona-albumen layer an unknown parasitic organism which has adversely affected its development.

The blastoderm has a circumferential extent of about 4.2 mm., and so should be intermediate between VVH 42 and *Echidna* IV in its stage of development, but it is much nearer the latter, since it possesses deep as well as intercalated primitive endoderm cells (Pl. XXVI, fig. 173, *pr.end.d.*). Its structural characters, however, indicate that it had already ceased to grow and that it would have failed to complete the normal course of development. Its condition is in all probability due directly or indirectly to its infection by a curious parasitic organism, the precise systematic position of which we have so far been unable to determine. Dr. C. M. Wenyon, F.R.S., who has been good enough to examine the sections, is of the opinion that it is probably not a Protozoan but a fungoid organism, since the "spores" are quite unlike those of any parasitic Protozoan known to him.

The main part of the infection (Pl. XXVI, fig. 174), consisting of numerous large cyst-like bodies and innumerable minute "spores," lies imbedded in the zona-albumen layer peripherally to the germ-ring, at the far side of the sections which comprise only the upper hemisphere of the egg. The zona-albumen layer has become split into two sheets, between which the structures mentioned form an elongated loose mass, about 0.56 mm. in length by about 0.072 mm. in thickness (Pl. XXVI, fig. 174), which extends upwards from the cut edge on the far side of the sections, to terminate a short distance from the germ-ring. The "spores," however, continue on in the zona-albumen layer for a distance of over 1 mm. towards the upper pole as a disconnected sheet, one "spore" thick (Pl. XXVI, fig. 174, *za.*). Cyst-like bodies also seem to occur in small numbers in the superficial yolk of the egg on the infected side, and we have also observed a few "spores" imbedded in the zona-albumen layer on the opposite (near) side of the sections.

The cyst-like bodies, oval or sometimes rounded in outline (Pl. XXVI, fig. 174, *cys.*), vary in diameter from  $0.011 \times 0.010$  mm. to  $0.040 \times 0.033$  mm. (in one instance  $0.054 \times 0.037$  mm.), but are mostly of the order of  $0.036 \times 0.033$  mm. in diameter, with a thickness of about 0.020 mm. Each is enclosed in a definite wall, inside which and apparently composed of the same material is a coarse reticulum enclosing spaces of quite irregular size and, so far as we have observed, entirely devoid of contents. The relationship of these structures to the "spores" is quite obscure.

The "spores," which occur in large numbers intermingled with the cyst-like bodies, are minute oval or rounded structures (Pl. XXVI, fig. 174, *sp.*). Each possesses an enclosing membrane, inside which is a clear matrix with up to six or more deeply staining granules situated peripherally in it. They vary in diameter from 0.003 mm. to  $0.0045 \times 0.003$  mm. (exceptionally reaching  $0.006 \times 0.0045$  mm.). Those which have penetrated into the zona-albumen layer away from the main mass are often flattened and more elongated, some of them measuring up to  $0.008 \times 0.0016$  mm. Amongst them there are present quite minute deeply staining "spores," suggestive, as Dr. Wenyon has pointed out to us, of the occurrence of a process of multiplication by budding, but of this we have yet to obtain definite evidence.

Lastly, we have to mention the occurrence amongst the cyst-like bodies of small numbers of oval or rounded "spore-aggregates," as we may term them, measuring up to  $0.033 \times 0.024$  mm. in diameter (in one case the "spores" are arranged more or less radially around a minute central lumen), and we

have observed at least one thin-walled cyst with its interior completely occupied by what appears to be coarsely granular material, no reticulum being present (Pl. XXVI, fig. 174, *cys*<sup>1</sup>).

As concerns the blastoderm itself, the constituent cells of its central region overlying the yolk-bed, apart from some lack in staining capacity, appear reasonably well preserved and normal looking (Pl. XXVI, fig. 173). The cells of its peripheral region, on the other hand, have stained very poorly, and at both margins of the blastoderm show obvious signs of degenerate change. Here, over a width of five cells or so, extending inwards from the germ-ring, the cells are small and shrunken, with glassy-looking cytoplasm and pycnotic nuclei. The germ-ring itself is poorly developed and poorly stained, and its nuclei are shrunken and pycnotic. Moreover, nowhere throughout the extent of the blastoderm have we encountered any signs of mitotic activity.

It seems clear from the evidence that the peripheral growth of the blastoderm had entirely ceased some time before the egg was preserved.

Finally, in this connection we may draw attention to the fact that the deleterious influence of the parasite on the blastoderm and germ-ring has not been limited to the parts of these structures immediately adjoining the main site of infection but has spread throughout their extent, right round the circumference of the egg.

It remains to be mentioned that the prospective ectodermal cells are mostly fusiform and that deep as well as intercalated primitive endoderm cells are present but are not very numerous. The deep cells are mainly located below the central region of the blastoderm, many of them being large and spheroidal (Pl. XXVI, fig. 173, *pr.end.d.*); very few are present in the peripheral region.

A small number (four or five) of more or less flattened pycnotic *yolk-bed nuclei* is present, lying in contact with the yolk-membrane, below a slight depression in the central region of the yolk-bed.

*Echidna* XII. (Pl. XXVI, fig. 175).

(Diameter of egg, 4.0 mm. (fresh). Fixation, PNO.)

This egg, like *Echidna* XVIII (*ante*, p. 79) was sectioned with the shell *in situ*. The sectional plane is oblique to the egg-axis and the sections themselves are somewhat broken, but they suffice to show that it approximates to *Echidna* XVIII in its stage of development.

The circumferential extent of the blastoderm is approximately 8.5 mm., that of the lower polar area 3.15 mm. The *pr. end.* cells are well developed (Pl. XXVI, fig. 175) and many of the deep cells are provided with distinct processes.

We make reference to this egg here for the reason that it gives us the opportunity to illustrate what we take to be the remains of the outer more fluid layer of the albumen coat of the egg (Flynn and Hill, 1939, Part IV, pp. 541-542, C. J. Hill, 1941, Part V, pp. 5-8) of which previously we had observed traces only. Comparable remnants of this layer are also present in *Echidna* XVIII.

In Pl. XXVI, fig. 175, it will be seen that outside the compact zona-albumen layer (*za.*) there is present a number (up to five are visible in the figure) of fine laminae (*la.*) separated by spaces in which occur quantities of a finely granular material, sometimes (especially in the space between the laminae and the shell) presenting an irregular net-like appearance (*cgm.*). We suggest that these laminae and the intervening coagulum together represent the outer more fluid



layer of the albumen coat of the egg. The dense albumen layer, to the under-surface of which the very thin zona is closely adherent, varies in thickness over the upper polar region from 0.009 to 0.010 mm. It stains deeply with eosin, as do the laminae in question, and in this egg presents only slight traces of lamination.

In *Echidna* XVIII, the zona-albumen layer over the upper polar region attains a greater thickness (0.012 to 0.018 mm.) than in *Echidna* XII, and consists of a compact deep zone and a finely laminated superficial zone, which merge gradually into each other. On its outer side the latter zone passes over into a series of rather coarser laminae, separated by narrow spaces containing coagulum as in *Echidna* XII.

In both eggs these supposed remains of the more fluid albumen layer are only found well preserved over restricted areas of the upper hemisphere, and are absent over the lower polar region where the zona-albumen layer is thinner than elsewhere.

The shell in *Echidna* XII has a thickness of about 0.012 mm., which compares with a thickness of 0.011 mm. in *Echidna* XVIII (*v.* in regard to structure, Hill, 1933, Part II, pp. 446 & 447, figs. 39 & 40, Pl. 33).

## FINAL SUMMARY AND DISCUSSION.

A synopsis of the chief phases in the ontogenesis of the primary germ-layers, as revealed in our Groups I–V, is provided on pp. 3–4, whilst a summary of our observations on the later stages of cleavage, comprised in Group I, is given on pp. 29–33. Here we may accordingly limit ourselves to a brief review and discussion of the more important of the observations and conclusions set forth in detail in the preceding pages relating to the formation and growth of the blastoderm and the establishment of the primary germ-layers in the Monotremata.

### A. FORMATION AND GROWTH OF THE BLASTODERM.

#### 1. *The Germ-ring.*

One of us in a paper published over thirty years ago (Hill, 1910) provided a summary of our then existing knowledge of the early development of the Monotremata, in the course of which it was stated that no nuclei are recognizable in the yolk underlying the blastodisc, “nor is there ever any trace of a syncytial germ-wall, features in which the Monotreme egg differs from the Sauropsidan” (p. 87). We are now, however, able to show that free cells (sub-disc cells and vitellocytes) do occur in the yolk-bed, below and around the blastodisc, and we have adduced strong reasons (*v.* pp. 30–31) for regarding them as homologous with the merocytes or yolk-cells of the Reptilian egg. We are further able to demonstrate that a nucleated syncytial ring (the germ-ring) does eventually become established around and in contact with the periphery of the blastodisc, though this ring is in no way comparable with the germ-wall of the Reptilian blastodisc as usually defined, the latter being cellular and not a syncytial thickening (*v.* pp. 6–7).

We have shown that the germ-ring, on whose presence and proper functioning the whole future course of development seems to depend, takes the form, when fully established, of a continuous richly nucleated band of cytoplasm of somewhat varying width which completely encircles the blastodisc, the main part of it

extending from the disc-periphery outwards, but it also runs inwards for a very short distance below the latter. It attains its greatest thickness immediately adjacent to the disc-margin and rapidly thins out on both sides. It varies considerably in width and in thickness from disc to disc and even in the same disc: *e.g.* in VVH 6 of Group III it has a width of about 0.12 mm. and a thickness of 0.024 to 0.03 mm.; in VVH 3 of Group V its width ranges from 0.18 to 0.21 mm. and its thickness from 0.018 to 0.024 mm.

Structurally, it consists of a layer of granular cytoplasm, more or less clearly distinguishable into two zones: (*a*) a denser, more deeply staining superficial zone which thickens to contain the nuclei, being here only slightly vacuolated but becoming more coarsely vacuolated in its thinner peripheral region, and (*b*) a deep zone of lighter staining reticular cytoplasm enclosing numerous fine yolk-granules and small yolk-spheres, and with a quite irregular uneven under-surface, owing to the presence of prolongations which extend down, between and around the sub-jacent yolk-spheres. As in its progenitors, the vitellocytes, these prolongations are in continuity, at all events at first, with the cytoplasmic reticulum of the under-lying yolk. Its nuclei are usually situated in its thicker region, adjacent to the disc-margin, and are fairly numerous and often large.

Whilst the under-surface of the germ-ring is quite uneven and devoid of a definite boundary-line, its upper surface, intimately invested by, or fused with, the egg-membrane, is perfectly well defined, and may present a continuous even contour, in which case that part of it adjacent to the disc-margin is simply overlain by the peripheral disc-cells or it may be depressed close to the disc-margin to form a gutter-like groove in which the peripheral cells are situated. The peripheral disc-cells, however, do not simply rest on the surface of the germ-ring. On the contrary, they are intimately connected with it, either by the close adherence (practically amounting to fusion), of their cell-membranes to its surface, where they make contact, or the disc-cell may establish direct continuity with the germ-ring by means of a very thin lamellar prolongation from the outer end of its cell-body which fuses with the surface of the ring, or when the latter is grooved, with the edge of the ridge bounding the groove.

Our observations show that the germ-ring is a syncytial structure which is formed as the result of the enlargement, concentration and fusion of the peripheral and sub-marginal vitellocytes around and immediately below the periphery of the blastodisc. Its formation is already well initiated in the youngest member (VVH 35) of Group III, in which the blastodisc has reached its maximum development and is six to seven cells thick centrally.

In this disc, over rather more than half its perimeter, the ring has been established as a continuous formation, varying in width from 0.10 to 0.23 mm. and in maximum thickness up to about 0.018 mm., whilst over its remainder, the vitellocytes there present, both peripheral and sub-marginal, are large, binucleate or multinucleate and are in process of becoming linked up by cytoplasmic connections, preparatory to their complete fusion. In the succeeding blastodisc, VVH 27, the germ-ring is present all round the disc but is thin, and over parts of its course becomes reduced before reaching the disc-margin. In the next following stage, VVH 14, it is much thicker and may be said to be fully established, and the same holds true for the connections of the peripheral disc-cells with it.



## 2. *Transformation of the Blastodisc into the Blastoderm.*

The effect of the formation of the germ-ring on the blastodisc is extremely striking, especially when the series of stages comprised in Group III is considered as a whole; for the disc immediately begins to increase in surface-area, and from a diameter of  $0.56 \times 0.56$  mm. and a thickness of 0.136 mm. in VVH 35, it has increased in the end-member of the series, VVH 6, to a diameter of  $1.36 \times 1.38$  mm., whilst its thickness has become reduced to 0.032 mm. This growth is apparently induced by the germ-ring. The vitellocytes, as we have shown, possess the power of migration, and this same capacity would seem to be retained by the germ-ring. As soon as it is completed it begins to migrate outwards over the yolk, in close contact with the egg-membrane, and the intimate connection of the peripheral disc-cells with its surface somehow or other induces a response on the part of the blastodisc as a whole. It increases in surface-extent and at the same time decreases in thickness, and so, as the peripheral migration of the syncytial ring proceeds, it gradually becomes transformed from a thick, compact, biconvex disc into a relatively thin membrane or blastoderm, such as is seen in *Echidna* 30, which occupies the mid-position in the Group III series. Here the blastoderm has attained a diameter of  $0.96 \times 1.0$  mm., whilst its maximum thickness is no more than 0.032 mm., a noteworthy decrease as compared with VVH 35 (see above). It is 2 (occasionally 3) cells thick centrally as compared with 6–7 in the latter, whilst peripherally it is formed of a layer 1 cell thick, with only occasional deep cells below it.

Unquestionably the peripheral growth of the blastoderm and the peripheral migration of the germ-ring are closely inter-related phenomena which mutually react on each other, and though the suggestion made above, to the effect that the germ-ring plays a predominant rôle in initiating and controlling the growth of the blastodisc, may seem to over-emphasize the importance of that structure, it does receive support from the very interesting anomaly we have encountered in Group V (v. p. 97). The egg in question (*Echidna* IX) possesses a blastoderm which developmentally belongs to that group, but it measures only 2.14 mm. in diameter and has clearly been arrested in its growth. When we first examined this egg, we concluded that the explanation of this arrest was to be found in the presence of small groups of cells over-lying the junction of the blastoderm with the germ-ring, which, we presumed, had exerted an inhibitory influence on the migratory activity of the latter. But after further consideration of all the details and in view especially of the poor development of the germ-ring itself, we now think it more probable that the cells in question are the result and not the cause of the retardation in the activity of the germ-ring, and that this retardation is due to some inherent defect in that structure itself. Whatever the cause, it is clear that in this egg the germ-ring has failed to continue to migrate outwards over the yolk in normal fashion and that as a consequence the blastoderm has been unable to extend and reach the dimensions commensurate with the stage of development it has attained.

The peripheral migration of the germ-ring and the correlated peripheral growth of the blastoderm continue until the yolk-mass of the egg is completely enclosed, the final point of closure being marked by a cicatricial thickening at the lower pole, the yolk-navel, in the formation of which the ectoderm and the germ-ring

both participate. In our material, what we take to be the first appearance of the yolk-navel was observed in surface view in *Echidna* I of Group V (v. p. 88). Its structure is described in two early primitive streak stages of *Echidna* (v. pp. 94-96), and a comparison with the Reptilian navel, which brings out interesting points of agreement in the two, is instituted below.

The completion of the enclosure of the yolk-mass of the egg by the bilaminar blastoderm marks an event of the greatest developmental significance, inasmuch as thereby the egg has become converted into a potential blastocyst or blastodermic vesicle (that typically mammalian developmental stage) which is capable of absorbing the rich nutritive fluid secreted into the uterine lumen by the uterine glands and of increasing of size. In this way it is capable of providing the space as well as the additional nutritive material necessary for the development of the embryo up to the time of hatching, *i.e.* during the later intra-uterine and the incubatory periods of its life-history.

The rapidity with which the enclosure of the yolk-mass is effected in the Monotreme is a noteworthy feature, though Peter (1934) has recorded an almost equally rapid enclosure in the egg of the Chameleon, where it is almost or already completed at the time of appearance of the ammion, when the blastoderm is still two-layered. In the egg of the Lizard, on the other hand, Peter states that enclosure proceeds much more slowly and is not completed until the embryo has reached the 24-somite stage. In the case of the Tortoise, Clark (1857) has stated that the entire yolk is completely enclosed by the blastoderm already in the "gastrula stage."

### 3. *The Marginal Region of the Sauropsidan Blastoderm and the Homology of the Germ-ring.*

Whilst the evidence (v. pp. 30-31) appears to substantiate the conclusion that the vitellocytes of the Monotreme are the homologues of the merocytes or yolk-cells of the Reptilian egg, there still remains the question whether the germ-ring to which they give origin is represented in the latter. In other words, has the germ-ring arisen *de novo* within the limits of the Monotremata or is it an inheritance from their Reptilian ancestors? In the present state of our knowledge, it is not possible to provide a positive answer to these questions.\* No detailed study, so far as we know, has ever been made of the mechanism of the growth of the Reptilian blastoderm over the yolk, and only one observer, H. Virchow (1892 *b*), appears to have concerned himself with the details of the structure of its marginal region.

Virchow's observations are of considerable interest. In his stage II ("beginnende Gastrula") of *L. agilis*, he described and figured (fig. 17, Pl. 4) a superficial layer of cytoplasm situated just outside and abutting on the margin of the blastoderm, which he termed "das oberflächliche Protoplasma" (p. 53). According to his description, this layer, thick where it adjoins the blastoderm margin, rapidly thins out as it is traced outwards, and continues as a thin lamella for an indeterminate distance over the surface of the yolk.

Virchow states that small isolated cells are frequently to be found enclosed in the thicker marginal part of the layer. One such cell (labelled a "Randsaumzelle")

\* See, however, the discussion of the marginal region of the blastodisc in Birds, below.



or marginal cell) is present in the section illustrated in his fig. 17, and up to three may occur in a single section. He rejects the idea that these cells are given off from the merocytes and become added to the margin of the blastoderm, and inclines to the view that they are marginal cells of the latter, which, pushing outwards, have become secondarily enclosed in the superficial protoplasm, a highly improbable occurrence as we think; in spite of Virchow's opinion, it seems to us much more likely that the cells in question are actually merocytes. He further states that the layer itself is in direct continuity with the protoplasm of the merocytes situated below the margin of the blastoderm, and is also connected by fine vertically-running processes with an underlying cytoplasmic network in the yolk, which he terms "the peripheral protoplasm," from which fine processes penetrate downwards between the yolk-spheres. This network is said also to be in direct continuity with the protoplasm of the marginal merocytes, so that the peripheral protoplasm, he points out, could be described as the continuation of the merocyte-layer, without thereby implying that it originates from the latter. The question of the source and significance of these two cytoplasmic formations, superficial and peripheral, Virchow leaves quite open. He states that the fate of the marginal merocytes, which occur both below and peripherally to the margin of the blastoderm, is unknown, but he records the interesting observation that they migrate distally simultaneously with the growth of the blastoderm over the yolk, and that in this way they certainly reach as far as the equator, perhaps indeed to the distal pole, since in one case he observed small protoplasmic masses at that pole which resembled plasma-rich merocytes, though no merocyte nuclei were seen (1892 *a*, p. 202).

Confirmation of the existence of a superficial cytoplasmic layer immediately adjoining the margin of the blastoderm (the marginal cytoplasmic zone as we may term it) is provided by Will (1895) in his paper on the formation of the germ-layers in *Lacerta* (see his fig. 28<sup>c</sup>, Pl. 4, illustrating a section through the germ-wall) and also by Hrabowski (1926), who mentions that she observed a layer of cytoplasm forming an extension of the marginal cells of the blastoderm ("als Vorläufer der letzten Randzellen der Keimhaut," p. 317) in an early developmental stage of *L. agilis*.

Virchow's observations are of particular interest in relation to our own, inasmuch as his peripheral protoplasmic network strikingly recalls the cytoplasmic reticulum which pervades the yolk-bed and its marginal zone in the Monotreme egg, whilst his superficial layer of protoplasm (with its enclosed "cells") occupies a position which corresponds precisely with that of the germ-ring in the Monotreme. That being so, it is unfortunate that our knowledge of this marginal cytoplasmic layer in the Reptile is so fragmentary. Nor have we any certain knowledge of the nature of the cells which, according to Virchow, become enclosed in it. May it not be that it is simply the equivalent of the peripheral cytoplasmic layer of the Monotreme ovum (*v.* Part IV, p. 466), here locally thickened where it adjoins the margin of the blastoderm, and that the "enclosed cells," as we have suggested above, are none other than yolk-cells or nuclei which have secondarily migrated into it?

Since the above was written, we have been able to examine the structural relations in the marginal region of the blastodisc in the Bird, and to consult the

relevant literature. The facts thus revealed appear to be in accord with the interpretation implied above.

Although the existence of nuclei ("Dotterkerne") and of a so-called syncytium ("Dottersyncytium") in the white yolk underlying and surrounding the blastodisc in the Fowl was for long recognized by the earlier investigators, it was not until the publication of the work of Mary Blount in 1907, on the early development of the Pigeon's egg, that our knowledge of the marginal region of the Bird's egg can be said to have reached some degree of precision.

Blount was able to show that the blastodisc, from the stage of the unsegmented disc onwards, is surrounded by a narrow marginal zone of cytoplasm containing fine yolk-granules, which, in section, is seen to be in continuity, like the disc itself, with the underlying white yolk. It can be traced outwards beyond the disc-margin for some little distance, and it can also be followed inwards, below the margin of the disc into continuity with a somewhat similar zone which constitutes the superficial layer of the white yolk-bed and which is destined to form the floor of the sub-germinal cavity when that appears.

Blount utilized the term periblast (Agassiz and Whitman, 1884) to designate these zones, distinguishing them as the marginal and central periblast respectively. They would seem to correspond to the peripheral and central "Dottersyncytium" recognized by H. Virchow (1892). The fact should be emphasized that the prospective marginal periblast is not a separate entity but is from the first continuous, on the one hand, with the germinal disc and on the other with the thin peripheral cytoplasmic layer underlying the egg-membrane. It is to be regarded simply as the peripheral portion of the disc-primordium, which does not become involved in the definitive cleavage process.

According to Blount's account, after the cessation of the transient accessory cleavage induced in the inner part of the marginal periblast by the supernumerary sperm-nuclei and the disappearance of the latter, the large marginal cells of the disc pass once more into continuity with the marginal periblast, though only temporarily. These cells have meantime ceased dividing to form central cells, but their nuclei continue to divide, and some of the peripherally situated daughter-nuclei move out into the marginal periblast "about eleven or twelve hours after fertilization," and there furnish, according to Blount, the whole of the periblast nuclei. They divide actively, and not only spread throughout the extent of the marginal periblast but also migrate inwards below the disc, into the central periblast, though they are said not to penetrate into the funnel-shaped central core of the yolk-bed into which the latebral neck expands (the so-called nucleus of Pander).

Blount regards the periblast as a syncytial formation and holds that it plays a highly important rôle in the growth of the blastodisc since both the central and marginal periblast contribute cells to it. It constitutes, in her view, the primordium of the germ-wall.

We have examined the marginal region in a series of early blastodiscs of the Sparrow and are able to confirm the existence in this bird, also, of a well-developed marginal cytoplasmic zone (the marginal periblast of Blount) and a corresponding central zone underlying the sub-germinal cavity, but we have no blastodiscs early enough to show how the nuclei in these two zones originate, whether exclusively



from marginal cell-nuclei as Blount maintains or partly from these, partly from the nuclei of deep disc cells prior to their separation from the yolk-bed or exclusively from the latter as most of the older workers assumed.

The marginal zone in the Sparrow varies somewhat in extent and in appearance in different discs. In Sp. 6.17 S (disc about 2.01 mm. in diameter  $\times$  0.013 mm. in thickness), for example, the zone is easily recognizable as a clear finely alveolar layer of cytoplasm abutting on the disc-margin and rapidly thinning outwards. It attains its maximum thickness (about 0.030 mm.) close to the disc-margin, but at a distance of 0.15 mm. from the latter it is no thicker than 0.006 mm. Beyond this point it continues on below the egg-membrane as a very thin layer but exhibiting occasional irregularly disposed thicker patches. It contains fairly numerous fine yolk-granules only lightly stained, so that the zone stands out with exceptional clarity. It is invested on its upper surface by the egg-membrane and passes over below, without limit, into the underlying fine-grained yolk, which here and there is prolonged up into it. Relatively few nuclei are present in the zone; they vary in size up to a diameter of  $0.012 \times 0.009$  mm. and occur singly or in twos, more rarely in groups of from four to six.

Highly characteristic of the marginal zone here and in other discs is the presence in it of oval or rounded vacuolar spaces, as many as four or five occurring together in one section. In other discs they may be so large as to bulge down into the underlying yolk (Pl. XXVII, fig. 179, *vsp.*). Such spaces are also well known in the Pigeon and Fowl.

In Sp. 48 (disc about 1.80 mm. in diameter  $\times$  0.064 mm. in thickness), the marginal zone is easily traceable outwards from the disc-margin for a distance of 0.320 mm., its maximum thickness close to the latter being about the same as in the preceding egg (0.030 mm.). It differs from that of the latter in being richer in fine yolk-granules, whilst its nuclei are more numerous and attain a much larger size, the large nuclei lying in cytoplasmic areas free from granules.

In Sp. 2 (Pl. XXVII, fig. 179), the marginal zone is remarkably well developed, presenting, in the section figured, a striking superficial resemblance to the germ-ring of the Monotreme. The disc measures about 2.29 mm. in diameter  $\times$  0.08 mm. in thickness and is at a stage prior to delamination, as also are the two discs referred to above.

The figure shows the marginal region of the disc and the immediately adjoining portion of the marginal zone in section. It will be seen that the relatively small peripheral disc-cell (*pdc.*) rests in a slight depression on the surface of an elongated band-like area of cytoplasm (*ca.*<sup>1</sup>), in which is situated, immediately below *pdc.*, a row of four nuclei. This area, appearing at first sight like a large multinucleate cell, is the sub- and juxta-marginal portion of the marginal zone. It is composed of dense cytoplasm devoid of yolk-granules, except immediately below the egg-membrane covering its upper surface and at its apparent peripheral border. It does not end here, however, but passes by way of a light staining area of alveolar cytoplasm into a second, less extensive, area of dense cytoplasm (*ca.*<sup>2</sup>) containing a nest of seven or more nuclei. This area appears to terminate peripherally by spreading out to form the boundary of the large vacuolar space (*vsp.*) which occupies the left (lower) corner of the figure. Actually it continues on as a very thin layer, roofing over this space as well as a second smaller space lying immediately to its

outer side. Beyond this it is traceable peripherally for a distance altogether of about 0.28 mm. measured from the peripheral disc-cell. It then becomes so thin as to be hardly recognizable in the sections. The maximum thickness of the zone in the region of areas *ca.*<sup>1</sup> and *ca.*<sup>2</sup> is about 0.016 mm.

Traced centrally below the marginal region of the disc, area *ca.*<sup>1</sup> is seen to pass into a short segment rich in fine yolk-granules. This is succeeded by a third cytoplasmic area (*ca.*<sup>3</sup>), almost devoid of granules, in which, in the following section, is a nest of one large and three or four smaller nuclei. If we arbitrarily reckon area *ca.*<sup>3</sup> as belonging to the sub-marginal portion of the marginal zone, the central zone may be said to follow on from its central end.

The central zone, invested on its surface by the yolk-membrane, forms the floor of the sub-germinal cavity but extends peripherally beyond it. It consists of two portions, a peripheral region in continuity with the marginal zone and a central region formed by the central core of the yolk-bed (nucleus of Pander). The central zone as a whole is more uniformly rich in fine yolk-granules than is the marginal zone. In its peripheral region the granules are more compactly arranged and on the whole rather coarser than those in the central region, and pass by gradual transition into the underlying white yolk.

Like the marginal, the central zone possesses a cytoplasmic basis, but here it takes the form in the main of a delicate reticulum in which the yolk-granules are situated. This reticulum is readily visible in the central core where the yolk-granules are more dispersed than in the peripheral region. In the latter it is more difficult to observe, but traces of it can often be seen immediately below the yolk-membrane in small areas where the yolk-granules are sparse or absent. In addition, in the peripheral region (more rarely in the central core, as in Sp. 48), there are present numbers of yolk-free cytoplasmic areas varying considerably in size and each enclosing a very varying number of nuclei (from one to twelve or more). Below the peripheral region of the disc such areas are often fairly large, resembling those in the marginal zone, but elsewhere the cytoplasm tends to be less abundant and may indeed be reduced to a quite thin film investing the nuclear nest.

It is, of course, the nuclei in these cytoplasmic areas of the marginal and central zones which form the "yolk or periblast nuclei" of authors.

Here, then, in the marginal region of the blastodisc of the Bird, we venture to suggest, we have exemplified a structural condition (which very probably obtains also in the Reptile) out of which, as a basis, the germ-ring of the Monotreme may well have originated. We have only to postulate a marked reduction of the marginal zone (consequent possibly on the progressive reduction in size of the egg and a greater concentration of its cytoplasm in the germinal disc proper) and a continuation of activity on the part of the marginal cells in the production not of "yolk-nuclei" merely as in the Bird but of "yolk-cells or merocytes" as in the Reptile, possessing an all but completely independent cellular status. Such "cells," we suggest, may well have formed the forerunners of the vitellocytes of the Monotreme (themselves the product of the marginal cells of the blastodisc) out of which the germ-ring came to be built up in the site of, and in substitution for, the marginal cytoplasmic zone.

We suggest, accordingly, that the germ-ring is not a neo-formation which has arisen within the Monotreme group but has been evolved from structural conditions pre-existing in the egg of their Reptilian ancestors.



4. *The Yolk-navel in the Reptilia in comparison with that of the Monotremata.*

The occurrence of a yolk-navel in Reptiles is well known and its structure has been described in more or less detail by a number of observers, including Virchow (1892 b), Assheton (1910), Hrabowski (1926), Peter (1934), Boyd (1942).

Virchow's observations on the yolk-navel ("das Polster der distalen Poles," as he terms it) of *L. agilis* show that in his stage IV, in which the yolk is said to be almost completely enclosed, there is present at the lower pole of the egg a slight depression which is bounded by the thickened margin of the blastoderm (figs. 27 & 28, Taf. 4). The depression is clothed by a layer, apparently protoplasmic, which, when well developed, is uniformly thick and distinguishable into a thin, very compact, superficial zone (apparently of a cuticular nature) and a thicker, finely reticular, deep zone which is sharply delimited from the yolk but is beset by fine processes and includes fine yolk-granules. In the succeeding stage VI, the definitive navel is present in the form of a knob-like granular mass which projects upwards into the yolk and is beset on its inner and outer sides by numerous yolk-free cells (fig. 30, Taf. 4). These latter, Virchow supposes, may have originated from the blastoderm-margin, whilst the knob-shaped mass is evidently derived from the above-mentioned layer lining the original navel depression, and that layer itself, the author suggests, may have originated from the "peripheral protoplasm," under which expression he presumably includes both his "superficial and peripheral protoplasmic layers" (v. pp. 105-106).

Peter (1934), in his account of the yolk-navel of the Chameleon (*C. vulgaris*), describes the yolk of the navel-area as being clothed by a "plasma-layer" which is similar to that described by Virchow in possessing a superficial zone which he regards as of the nature of a "cuticula." As the thickened margin of the blastoderm closes in, the plasma-layer becomes invaginated to form a relatively thick folded layer enclosing a well-marked cavity opening outwards. When closure is finally effected, this layer forms, along with the marginal thickening of the endoderm, a crumpled mass underlying the now continuous layer of ectoderm.

Hrabowski's very extensive observations show that in the forms she investigated (*Lacerta agilis*, *L. vivipara*, *Anguis fragilis*), the yolk-navel is composed of three constituents, viz. a superficial ectodermal proliferation from the blastoderm-margin bordering the navel-area, a non-nucleated cytoplasmic layer (identical with that described by Virchow) bounding the navel-cavity, and a deep marginal endodermal proliferation which gives origin to a plug-like mass projecting inwards, so as to obliterate the outer part of the mentioned cavity. No mention of the navel-cavity is made by Virchow or by Peter, though it is clearly shown in his Abb. 5 (p. 161) of the Chameleon and also in his instructive Abb. 6 (p. 162) illustrating a section through the almost closed navel of the Lizard, in both of which it is seen to be bounded by the invaginated "plasma-layer." The latter figure also shows irregular proliferations from the marginal ectoderm and marked thickening of the marginal endoderm.

The Monotreme yolk-navel differs from that of the Reptile in two important respects: (a) The cytoplasmic layer is sparsely nucleated and (b) the endoderm, yolk-laden as it is, remains inactive. In Wilson and Hill's fig. 11, Pl. 5 of their specimen Y, it will be seen that the yolk-endoderm forms an all but continuous layer of normal character clothing the deep surface of the navel.

The navel-cavity, which we have described as occurring in the Monotreme navel, would seem to correspond, at least topographically, with that described by Hrabowski under the designation "Dotterlochsäckchen" in the yolk-navel of *L. agilis* and seen in Peter's Abb. 6, and also with the similar cavity described by Boyd (1942) in that of *Hoplodactylus maculatus*. In both these forms the cavity is described as being bounded by a thick layer of non-nucleated cytoplasm, evidently the same as that first observed by Virchow, lining the navel-depression and distinguishable, as he stated, into two zones, a thin, dense, superficial zone and thicker, finely granular, deep zone. It is formed by the invagination of the similar layer which, prior to the formation of the navel, clothes the exposed surface of the yolk in the navel-area. But none of the observers mentioned is able to show conclusively how this layer originates. Virchow, as we have stated above, thought it may have been formed from the "peripheral protoplasm." Hrabowski's view is not very clearly expressed, but she appears to suggest that it may be derived from the marginal cytoplasmic zone (Virchow's "superficial layer of protoplasm") which she observed in sections of an early blastoderm (v. p. 106). Boyd (1942, p. 72), in her description of the yolk-navel in the Gecko, *Hoplodactylus*, first of all expresses the view that its non-nucleated cytoplasmic layer is "evidently derived from the yolk-syncytium," but, apparently assailed by doubts, goes on to suggest that it may be derived from Virchow's "superficial protoplasmic layer" together with his "peripheral layer" or from a combination of these layers and the yolk-syncytium.

From the foregoing, it is clear that the evidence at present available is insufficient to enable us to affirm the strict comparability of the non-nucleated cytoplasmic layer in the yolk-navel of the Reptile with the germ-ring constituent in the navel of the Monotreme, notwithstanding the striking agreement in their topographical relations. We may remark, that we are not inclined to attach decisive importance to the apparent absence of nuclei in the Reptilian layer, since nuclei originally present may have degenerated and, moreover, the nature of the isolated "cells" which Virchow described as occurring in his "superficial layer of protoplasm" (v. pp. 105-106) and which he regarded as detached marginal cells, cannot be regarded as definitely established. We have suggested above (p. 106) that they are merocytes or yolk-cells.

##### 5. The Yolk-bed : Yolk-bed Cells and Nuclei.

###### A. Yolk-bed.

The yolk-bed is readily distinguishable from the remainder of the yolk-mass by its structural characters and its position at the upper pole of the egg. It is roughly triangular in form in section, its apex passing below into continuity with the laterobasal neck and its base, invested by the yolk-membrane, lying in contact with the under-surface of the blastodisc or with that of the central region of the blastoderm when the latter is established. Its basis is formed by a delicate cytoplasmic reticulum, varying greatly in its degree of distinctness in different eggs, in which are situated its constituent yolk-spheres and yolk-granules. The former are distinctly smaller than those of the yolk-mass and, peripherally and below, gradually merge into the latter.

In all cases we can recognize a fine-grained central region which passes by way of an intermediate zone into a coarser-grained peripheral region, and this in turn



gradually merges without limit into the still coarser yolk of the yolk-mass. But the central region varies considerably in the details of its structure from egg to egg. In the majority of eggs, directly above the junction of the lateral neck with the bed, there is present a conspicuous, more or less localized, light staining area, or central core as we may term it, which is richly and often coarsely vacuolated (Pl. III, fig. 21; Pl. XIX, fig. 115; Pl. XXII, fig. 146; Pl. XXIV, fig. 153). It contains more or less numerous fine yolk-granules, sometimes exclusively basophil, but more often very fine eosinophil granules occur intermingled with rather larger basophil granules.

This central core varies greatly in its dimensions, *e.g.* in *Echidna* IV it measures 0.40 mm. in width  $\times$  0.11 mm. in depth, the corresponding measurements in VVH 3 being 0.180  $\times$  0.048 mm. On the average its width is about 0.20 mm. and its depth 0.060 mm. In a few eggs, a more diffuse, vacuolated, superficial zone replaces the localized central core as in VVH 8 (Pl. XX, fig. 130), where it reaches a width of 0.50 mm. and a depth of 0.048 mm. VVH 32 is exceptional in possessing a superficial zone which is prolonged down into two diverging processes (about 0.09 mm. in depth), coarsely vacuolated and rich in very fine yolk-granules.

Peripherally and below, the central core merges into a vacuolated zone densely crowded with fine basophil yolk-spheres, the vacuolation being specially marked immediately above its junction with the lateral neck. In VVH 9, for example, there is present in this position a large vacuolar space 0.16 mm. in width  $\times$  0.08 mm. in depth, surrounded by smaller vacuoles.

Outside the central core and its surrounding zone the bed is formed by a region containing mostly small basophil spheres, and this gradually passes over into the peripheral part of the bed formed of still larger spheres.

As concerns the functional significance of the yolk-bed, we have little to add to what was said in Part IV. We have shown that in the early oocyte it contributes to the growth of the germinal disc, whilst in the later cleavage stages (from LC 3 onwards), yolk-spheres derived from the yolk-bed would seem to penetrate between the blastomeres, especially in the peripheral (junctional) region of the disc and to be ingested by them.

In this connection the characteristic non-nucleated bodies which we have described under the name of "yolk-balls" are deserving of notice. These structures are first encountered in the late cleavage stage, LC 7, and are met with in more or less abundance in later stages. They appear as small rounded or oval bodies, composed of a cytoplasmic matrix, often vacuolated and containing numerous fine basophil yolk-granules and small spheres. They may attain a diameter of up to 0.072  $\times$  0.036 mm. but are mostly smaller than this. They arise as bud-like projections from the surface of the yolk-bed, which eventually become free and are to be found lying in contact with the latter as well as between the cells of the blastoderm, and occasionally are to be met with actually at its surface. They are evidently of importance as a means of providing the rapidly growing cells with a supply of fine yolk.

Finally, the structural conditions obtaining in the central region of the yolk-bed, its extensive vacuolation, the vacuoles being presumably fluid-filled, and the presence in it of numerous fine yolk-granules, many of them chemically altered as indicated by their eosinophilic reaction, suggest that this region may be of functional importance as a centre for yolk-digestion.

## B. Yolk-bed cells and nuclei.

In the late cleavage stage, LC 4, we recorded (*ante*, pp. 18–20) the first occurrence of free cells in the yolk-bed, which we termed “sub-disc cells.” These cells, we suggested, owe their origin to the division of deep disc-cells. Some of them, we further suggested, eventually become incorporated in the disc, whilst others, which have migrated more deeply into the yolk-bed, may contribute to the “yolk-bed cells and nuclei” which are met with in very varying numbers in later stages and which we believe are derived in the main from inwandered sub-marginal vitellocytes. We also brought forward evidence which supported the conclusion that these cells and nuclei, as well as the vitellocytes, are homologous with the free cells known as merocytes, yolk-nuclei, etc. which occur in the yolk-bed in the Reptilian egg (*ante*, pp. 30–31). Details of their occurrence and structure are provided in the text, but a brief summary here may serve to emphasize the extent of their variability.

In the blastodiscs included in Group II, as in LC 6 and 7 of Group I, no yolk-bed cells were observed, but they reappear in Group III, where, out of eight blastodiscs, they are present in varying numbers in six, possibly represented by degenerate remnants in one, and absent altogether in another. In VVH 35, four cells are present, three of them multinucleate. One is very large ( $0.072 \times 0.050$  mm. in diameter) and possesses five nuclei of varying size. This cell is closely adherent to the yolk-membrane, below the central region of the disc. In VVH 27, six cells are present, one devoid of a nucleus, in the others the nuclei range from two to five. In VVH 14, only two cells are recorded, one multinucleate, the other minute and enucleated. In VVH 9 they are possibly represented by three quite degenerate remnants. *Echidna* 30 possesses at least five cells with poorly developed cytoplasmic bodies. In VVH 47 no yolk-bed cells were observed, whilst in VVH 45 some ten deeply eosinophil nuclei are present in the central region of the bed, of which six occur in one group. No cytoplasm is distinguishable around them but some of them are surrounded by a zone of altered eosinophil yolk-granules. VVH 6 is noteworthy for the presence of at least 27 nuclei, mostly of large size. Ten of them lie in the central region of the bed, in contact with or close below the yolk-membrane. The remaining 17 are situated in a large mass of eosinophil cytoplasm, lying just outside the central region, its upper surface being invested by the yolk-membrane.

In Group IV, VVH 32 possesses at least eight nuclei, together with the degenerate remains of a ninth. All are markedly eosinophilic, and in some of them the nuclear membrane is shrivelled and irregular. In VVH 42 only four nuclei were observed, one being small and shrivelled and another large ( $0.027 \times 0.018$  mm. in diameter).

In Group V we have been able to record yolk-bed nuclei only in two *Echidna* eggs out of seven. In VVH 28 they number about 18, ten occurring in one group. The nuclei lie in the peripheral part of the bed, for the most part close below the yolk-membrane, but a few are more deeply situated. They vary in diameter from  $0.007$  to  $0.030 \times 0.027$  mm. In VVH 11, eleven nuclei are present, of which eight lie in a mass of granular cytoplasm, situated immediately below the surface of the yolk-bed, just outside its central vacuolated zone.

These yolk-bed cells and nuclei do not appear to be of any developmental importance, whilst the variability in their occurrence and in their number when



they do occur rather discounts their being of any functional significance in relation to the organization of the yolk-bed. In the main they would seem to be derived from sub-marginal vitellocytes which migrated too far inwards below the blastodisc and so failed to become incorporated in the germ-ring during its formation.

## B. FORMATION OF THE PRIMARY GERM-LAYERS.

### 1. *The Constitution of the Blastoderm.*

The cardinal fact in the ontogenesis of the primary germ-layers in the Monotreme is furnished by the observation that in the four later blastoderms included in Group III (*Echidna* 30, VVH 47, 45 and 6), two distinct types of cell are present, distinguishable by their cytological characters and, as the succeeding stages show, with their destinies already determined. We have been able to follow these two cell-types through the stages comprised in Groups IV and V, and to demonstrate that they eventually segregate from each other to form two distinct layers respectively, superficial and deep, which constitute the primary germ-layers. We have accordingly designated the cells forming the two categories in question as the prospective ectodermal cells (pros. ect. cells) and the primitive endoderm cells (pr. end. cells) respectively. When they first become recognizable (in *Echidna* 30 and VVH 47), the blastoderm, about 1 mm. in diameter, is distinguishable into a thicker central and a thinner peripheral region and consists of a fairly well-defined superficial layer of cells, together with underlying deep cells. The latter are fairly numerous in the central region and are loosely arranged, one to two cells in thickness. In the peripheral region only sparse deep cells are present, except towards the margin where they are larger and more numerous.

The two cell-types exhibit no regular arrangement in the blastoderm but occur intermingled with each other throughout its extent. In the early blastoderms the pros. ect. cells greatly outnumber the pr. end. cells. They are the predominant cells in the superficial layer, and also occur as deep cells, especially in the central region. They are larger than the pr. end. cells and stain, on the whole, less deeply. Their cytoplasm is less densely, and rather more finely granular than that of the latter, exhibits a greater tendency to vacuolation and may contain small yolk-spheres. The nucleus is large (averaging about  $0.009 \times 0.008$  mm. in diameter) and stains rather lightly, though deeply basophil nuclei are also met with.

The pr. end. cells mostly occur singly or in twos and tend to be more individualized than the pros. ect. cells. They are definitely smaller and more deeply staining than the latter. Their cytoplasm is rich in granules, rather coarser than those of the pros. ect. cells, and usually stains deeply. It may be slightly vacuolated, but, curiously enough, only rarely are yolk-spheres present in it. The nucleus is smaller on the average than the pros. ect. nucleus (its diameter averaging about  $0.006 \times 0.005$  mm.) and it stains more deeply than the latter, being richer in nucleolar granules and possessing a coarser nuclear reticulum. Occasionally the nucleus is deeply basophil throughout, but in most the nuclear reticulum is intensely eosinophil, staining a darker tint than that of the pros. ect. nucleus. The outline of the nucleus often appears less regular and more angular than that of the latter, which is mostly oval or elliptical and characteristically plump with a smooth even contour. Mitotic activity is well in evidence in both categories of cell.

We have also recorded the existence in the blastoderm of a type of cell which in

the dimensions of its cell-body and nucleus approaches the pros. ect. type but in its cytoplasmic and nuclear characters approximates more to the pr. end. type. We have suggested that these cells which are not very numerous may be endodermal mother-cells. If they actually are such, they doubtless occur in still earlier blastoderms, but so far we have not been able to identify them with any certainty.

The two most advanced blastoderms in Group III (VVH 45 and VVH 6) are of special interest, inasmuch as the migratory cell movements which culminate in the establishment of the unilaminar blastoderm characteristic of the members of Group IV have in them already been initiated.

These two blastoderms are of practically the same size (in VVH 6,  $1.36 \times 1.38$  mm. in diameter  $\times 0.032$  mm. in thickness), but VVH 45 is slightly the earlier. In its central region the superficial layer is much less regular than in VVH 47 and the deep cells tend to be closely applied to its under-surface. In places, indeed, it is discontinuous, and here the deep cells actually reach the surface. In VVH 6 the superficial layer is still less well developed and is recognizable as an independent layer only in places and over quite short stretches, so that in contrast with VVH 47 the blastoderm over most of its central region has acquired the character of a laminar cell-aggregate mostly two cells thick. The appearances suggest that many of the more deeply situated cells are in process of crowding up amongst the surface-cells, and this is borne out by a careful study of the pr. end. cells, many of which can be seen insinuating themselves between the surface-cells, sometimes with the aid of short cytoplasmic processes, a fact of interest in view of the amoeboid activities displayed by these cells in later stages.

## 2. *First Phase : Formation of the Unilaminar Blastoderm.*

When we pass from Group III to Group IV, we find a profound and indeed remarkable change has been effected in the blastoderm.

In the interval between VVH 6 of Group III and VVH 32 of Group IV, the blastoderm has more than doubled in diameter (that of VVH 32 being about 2.9 mm.), and during that growth the deeply placed cells in the earlier blastoderms have all crowded up to the surface (a migration already initiated, as we have seen in the end members of Group III), and have become intercalated with the existing surface-cells to form a thin, perfectly continuous blastodermic membrane, a single cell in thickness.

The blastoderm has thus become genuinely unilaminar and in it the prospective ectodermal and primitive endoderm cells are fairly easily recognizable. The pros. ect. cells, by far the more numerous type in the blastoderm, are characterized by their relatively large size, their more or less flattened oval to fusiform shape and their light staining cytoplasm. The nucleus, oval to ellipsoidal in form, averages about  $0.010 \times 0.006$  mm. in diameter and like the cytoplasm stains rather lightly. The pr. end. cells are smaller than the ectodermal, their nuclei averaging about  $0.007 \times 0.006$  mm. in diameter, and they stain more deeply than the latter. They are also much more variable in shape, oval, fusiform, spheroidal, pear-shaped, oblong or quadrangular cells being met with. The cells lie intercalated in the blastodermic membrane singly or in groups of two or three, rarely more, and as the outcome of mitotic activity, which is still in evidence, they are more numerous than in VVH 6. Although there is as yet no evidence of active inward migration



on the part of the pr. end. cells, there are already indications that some few of them are on the way to acquiring the deep position, having become partially overlapped by the margins of adjoining ectodermal cells, and we have also encountered instances of the oblique division of a mother-cell, as the result of which the deeper of the two daughter-cells acquires its definitive position.

The occurrence of a unilaminar phase in the development of the Monotreme blastoderm was first observed by Semon (1894) in two eggs of *Ornithorhynchus* designated  $O_2$  and  $O_3$  and in one of *Echidna* ( $E_5$ ).

In  $O_2$  the blastoderm is described as covering about one-third of the surface of the egg, in  $O_3$  it reaches to within a short distance of the equator, and in  $E_5$  has reached the same. With only a very small number of early eggs at his disposal and no material at all between the blastodisc stage and that of the unilaminar blastoderm, it is not surprising that Semon completely failed to realize the significance of this condition, and in trying to interpret it, reached quite erroneous conclusions.

In his section of egg  $O_3$  he observed a slight depression in the blastoderm overlying the central part of the yolk-bed (Taf. IX, figs. 36 & 38), which he concluded had the significance of a blastopore, since he found an apparently similar depression in a corresponding position in the blastoderm of egg  $E_5$ , with below it a diffuse group of oval cells (about 15 appear in the figure) lying imbedded in the yolk-bed (Taf. IX, fig. 33). These cells, he presumed, had arisen by proliferation from the bottom of the depression, but of this there is not the slightest evidence in the figure and none is produced in the text and, indeed, is hardly to be expected in view of the extremely attenuated character of the cell-layer forming the blastoderm in this egg. Moreover, if such a proliferation had actually occurred, one would have expected to find the cells situated between the blastodermic membrane and the surface of the yolk-bed and not deeply imbedded in the latter, as shown in the figure. Semon, obsessed by the blastopore idea, nevertheless maintained that the proliferation he had postulated had the significance of a "Gastrulaeinstülpung" and that the cells so produced gave origin to the endoderm which he describes, correctly enough, in a later bilaminar blastoderm ( $E_7$ ) as consisting of a single layer of irregularly shaped cells, often connected only by their thin processes (Taf. IX, fig. 39). But he failed to explain how this continuous layer overlying the yolk came to be formed from a group of scattered cells originally situated deeply in the yolk-bed.

Our own observations demonstrate that the "cells" in question have nothing whatever to do with the formation of the endoderm, and though it is not possible from Semon's figure to determine their nature with certainty, we strongly suspect that what he observed in the yolk-bed were yolk-bed cells or nuclei.

The assumption by the blastoderm of the unilaminar condition is, we think, of significance both from the ontogenetic and the phylogenetic aspects.

Ontogenetically, we suggest, it really constitutes the first phase in the differentiation of the germ-layers, since it ensures that all the prospective ectodermal cells shall have reached their definitive position at the surface and, once that goal has been achieved, it only remains for the primitive endoderm cells to separate out and acquire an internal position below them. This they effect during the second phase, as subsequent stages show, mainly by a process of active migration inwards.

But how these cell movements are induced, in the case of the pr. end. cells, first in the outward direction and then in the opposite direction, inwards, we are unable to explain.

In the second place, from the phylogenetic aspect, it provides us with one of the most striking and fundamental agreements in the details of the early ontogeny of the Monotremata and the Marsupialia so far observed, to wit, the occurrence in the ontogeny of both these Orders of a unilaminar blastodermic membrane, composed of two types of cell, respectively ectodermal and endodermal in significance, which behave in precisely the same way in the two and eventually segregate to form the two distinct layers which constitute the primary germ-layers (*v. infra*, pp. 120–121).

### 3. *Second Phase : Formation of the Bilaminar Blastoderm.*

The stages comprised in our last group (Group V), in particular the eggs designated *Echidna* IV and XVIII, VVH 8, 3, 28, 11, *Echidna* I and *Platypus* S and SS, have enabled us to complete our account of the mode of formation of the primary germ-layers and to show how, as the result of the gradual segregation of the primitive endoderm cells below the superficial layer formed by the prospective ectodermal cells, the bilaminar blastoderm is derived from its unilaminar predecessor.

In the interval between VVH 42 (with the blastoderm about 3.28 mm. in diameter) of the preceding group and the youngest member of Group V, *Echidna* IV (with a blastoderm measuring about 5.5 mm. in circumferential extent), very definite advances have been effected in the structural constitution of the blastoderm, apart from its considerable increase in surface-extent. Much the most striking of these advances is manifested by the presence below the blastoderm of numbers of pr. end. cells. The blastoderm has accordingly lost its former unilaminar character and may now be described as formed by a superficial layer, composed of pros. ect. cells and still intercalated pr. end. cells, and by underlying dispersed pr. end. cells which have acquired their definitive deep position.

The pros. ect. cells which remain relatively passive in the superficial layer have also made progress. They are now more uniform in character than in VVH 42, and the majority of them have assumed their definitive form of large but relatively thin spindle-shaped elements with light staining cytoplasm and oval flattened nuclei, averaging  $0.011 \times 0.005$  mm. in diameter.

The pr. end. cells, as the result of active mitotic division, are much more numerous than in VVH 42 and, as just stated, many of them are now found lying in close contact with the deep surface of the superficial layer, others are still intercalated in the latter, and yet others, whilst still remaining in contact with the zona-albumen layer, have rounded themselves off, and so have become more or less isolated, preparatory to acquiring the deep position.

Our observations show that the pr. end. cells are endowed with amoeboid properties. They not only possess some power of movement, so that they can migrate bodily out of the unilaminar blastodermic membrane and so come to lie in contact with its deep surface, but they are also capable of sending out delicate cytoplasmic processes as well before but especially after their migration. That these are veritable pseudopodia is evident from the fact that in later stages the processes of adjoining cells can anastomose with each other and they may also



fuse directly with the cell-body of another cell. In this way the originally isolated cells become connected up into irregular cell-networks. Occasionally a cell still intercalated gives origin to such a process which closely underlies the deep surface of an adjoining cell, but the majority of the cells would seem to develop their processes only after they have reached their deep position.

The deep cells in *Echidna* IV occur, mostly singly or in twos, rarely more, widely dispersed below and in close contact with the under-surface of the blastodermic membrane. They vary somewhat in form but are mostly oval, ellipsoidal or spheroidal. Their cytoplasm is finely granular, frequently contains small vacuoles and stains rather deeply, as does the nucleus, which is large relatively to the cell-body (average diameter of the latter  $0.017 \times 0.008$  mm., and that of the nucleus  $0.009 \times 0.007$  mm.). The intercalated cells differ in no way structurally from the deep, but are more variable in their form. They occur singly as well as in groups of two or three and as pairs of sister-cells, whilst mixed groups of two, three or four cells (intercalated and deep) are also met with. Intercalated cells in mitosis are frequently encountered, but in this stage the deep cells have not yet commenced to divide actively.

Many of the intercalated cells appear at first sight as if they were in direct continuity with the adjoining pros. ect. cells, but more careful examination shows that this is an appearance only, due simply to close and intimate contact, and that the cells maintain their individuality throughout. This is brought out very clearly by other cells which have rounded themselves off and so become more or less isolated from the adjoining cells. This partial or complete freeing of the cells marks the first step towards their attainment of the deep position. Such an isolated cell may become deep, more or less passively, simply by the growth over it of the margins of the adjoining ectodermal cells and their eventual fusion, so that it becomes completely excluded from contact with the zona-albumen layer. On the other hand, the intercalated cell can itself become active and, utilizing its migratory capacity, can alter its form and gradually slide under the adjoining ectoderm cell, the advancing portion of the cell-body often presenting the character, though not the form, of a cytoplasmic process. But it does occasionally happen that the formation by the cell of a definite stout process much thinner than the cell-body and extending out below an adjoining ectodermal cell marks the first step in its migration. Furthermore, intercalated cells are met with not infrequently, dividing in planes parallel with, or oblique to, the surface, with the result that the deeper of the two daughter-cells in each case acquires its definitive position.

In *Echidna* IV the formation of cytoplasmic processes by the pr. end. cells is only just beginning, but in *Echidna* XVIII, with a blastoderm about 7.9 mm. in circumferential extent, many of the deep cells and some of the intercalated cells are provided with more or less well-developed processes, but as yet very few anastomoses have been formed between them.

The succeeding stages, VVH 8, 3, and 28, are all three characterized by a decrease in the number of intercalated pr. end. cells and a marked increase in the number of deep cells, due partly to continued emigration from the superficial layer, partly, indeed mainly, to active mitotic division on the part of the pr. end. cells, both intercalated and deep. In addition to widely dispersed mitotic activity, there is a definite tendency for specially intensive division to occur in localized spots, since

small groups of up to five or six cells are not uncommon, whilst in VVH 8, a few of the groups reach an exceptionally large size and comprise from 15 to 20 or more cells. The dispersal of the cells in such groups must again call forth the migratory powers of the cells, though in some cases dispersal may only involve their rearrangement into a single layer, the cells remaining in contact by their margins.

Many of the deep cells are now provided with well-developed cytoplasmic processes, some of them attaining a considerable length, and anastomotic connections between them are beginning to appear. The number of processes produced varies from cell to cell; there may be only one or up to as many as six and the form of the cell varies accordingly. The processes themselves are of very varying length and of very varying form, as is to be expected, seeing they are but temporary pseudopodial formations. They may be short and spike-like, elongated and tapering, or ending in a terminal expansion; they may be club-shaped or slender and slightly branched, and so on.

In VVH 11 the formation of anastomoses between the processes is much intensified, and in the tangential sections small groups of cells are to be seen so connected by their processes as to present the appearance of irregular loose networks. Numbers of apparently isolated cells provided with processes as well as spheroidal cells devoid of such are, however, still to be met with.

In *Echidna* I, the most advanced of the *Echidna* eggs included in the group, the blastoderm has made decided progress towards the attainment of the bilaminar condition. The great majority of the pr. end. cells have now reached their definitive position below the superficial layer, and many of them have assumed the form of more or less flattened fusiform cells, though ovoidal and spheroidal cells still occur in small numbers. As yet, however, the endoderm is far from being a connected layer, for, as the transverse sections show, there are small areas where deep cells are absent, other areas where scattered, apparently isolated, cells occur, and in yet other areas there are present small groups of four, five or more flattened fusiform cells connected by their margins so as to form cell-plates. Where such are present, the blastoderm can be described as bilaminar. In addition, examination of tangential sections yields evidence of the existence of cell-networks. We conclude, accordingly, that the endoderm in this stage is in process of taking on its final form, being represented by irregular cell-networks, occasional cell-plates and dispersed cells, all irregularly intermingled. By the linking up and consolidation of these components, a continuous sheet of endoderm is eventually established.

The final stage in the formation of the bilaminar blastoderm in the Monotreme, so far as our material is concerned, is illustrated by the most advanced member of the group, *Platypus* SS. In this egg the blastoderm over the greater part of the upper hemisphere (which alone is available for study) is genuinely bilaminar, though there still exist small isolated areas where the endoderm has not yet been completed. Where fully established, the blastoderm now consists of a superficial layer of ectoderm and an underlying layer of endoderm. The ectoderm is composed of large, flattened fusiform cells with oval flattened nuclei, averaging  $0.011 \times 0.005$  mm. in diameter, and so of much the same size as those of *Echidna* I. The endoderm consists for the most part of a similar type of fusiform cell, only smaller, the nucleus averaging  $0.009 \times 0.005$  mm. in diameter. Here and there, oval and spheroidal cells are met with incorporated in it, and such cells also occur in those



areas where the endoderm is still incomplete, whilst in the ectoderm overlying such areas an occasional pr. end. cell, still intercalated, may be encountered.

As is known, the endoderm in the Monotreme, from early primitive streak stages onwards, has the characters of a yolk-endoderm, *i.e.* it is formed of relatively large plate-like cells, polygonal in outline and crowded with discrete yolk-spheres of large size, which attains its maximum development in the extra-embryonal region of the blastoderm. The yolk-spheres are taken up secondarily, as we have been able to show in *Echidna* I, not by simple engulfment (the spheres being too large for that) but by a process of enclosure, the cell or cells (for sometimes two are involved) growing round the sphere until it is completely surrounded.

Our observations, accordingly, demonstrate conclusively that the primary germ-layers in the Monotreme originate as the outcome of a two-phase segregation of the two categories of cell (prospective ectodermal and primitive endoderm cells) which first become recognizable in the early blastoderm. During the first phase, all the deeply seated cells (both pros. ect. cells and pr. end. cells) crowd up into the surface-layer, with the result that the blastoderm becomes unilaminar and all the pros. ect. cells attain their definitive superficial position. In the second phase, the pros. ect. cells remain relatively passive at the surface, whilst the pr. end. cells, endowed as they are with amoeboid properties and capable of active division, gradually acquire their deep position, partly and mainly by active migration, partly by division in horizontal or oblique planes, and partly as the result of overgrowth by the ectodermal cells. Distributed below the superficial layer, singly and in small groups, they become joined up into irregular cell-networks by the anastomosing of the cytoplasmic processes to which they give origin, whilst small groups of cells come into contact by their margins to form cell-plates. From these cell-networks, cell-plates and isolated cells, a continuous layer of endoderm is eventually elaborated, whilst the ectodermal cells furnish a continuous layer of ectoderm; and so, in this way, the bilaminar blastoderm is established.

#### C. THE EARLY DEVELOPMENT IN THE SUB-CLASSES OF THE MAMMALIA.

From the phylogenetic point of view, as we have indicated above (p. 117), the most striking outcome of the present investigation is the demonstration of the fundamental agreement (amounting to practical identity) in the mode of formation of the primary germ-layers in the Monotremata and Marsupialia.

In the Marsupial, *Dasyurus*, one of us (Hill, 1910) has shown that the formative region of the blastocyst-wall is, from the first, unilaminar and composed of two categories of cell, prospective ectodermal cells and primitive endoderm cells ("entodermal mother-cells"). These two types of cell not only possess precisely the same prospective values but very much the same cytological characters as those of the Monotreme. As in the latter, the primitive endoderm cells of the Marsupial are smaller, more deeply staining, and less numerous than the ectodermal cells, and they are endowed with the same amoeboid properties. They are capable of migrating out of the unilaminar blastodermic membrane and of disposing themselves in close contact with its under-surface. Their pseudopodial processes, produced before as well as after their migration, then proceed to anastomose with each other, and the resulting cell-network later consolidates to furnish a continuous layer of endoderm. The prospective ectodermal cells, like

those of the Monotreme, are larger, more numerous and lighter staining than the endodermal. They remain passively at the surface, and when the emigration of the endoderm cells is completed they constitute a continuous layer of ectoderm.

This remarkable agreement in the details of the formation of the primary germ-layers in the two Orders affords still further and, indeed, most striking proof of the close phylogenetic relationship of the Ornithodelphian and Didelphian stocks.

But there is one important difference in the early ontogenetic phenomena in the two Orders to be noted. Whereas in the Monotreme the unilaminar blastodermic membrane comprises cells of the two categories distributed potentially throughout its entire extent and is devoid of any recognizable line of separation marking out the future embryonal and extra-embryonal regions, in the Marsupial a definite advance has been made, since the unilaminar wall of the spherical fluid-filled blastocyst is clearly distinguishable into two regions, sharply marked off from each other, viz. (a) an upper formative region, to which the two categories of cell above mentioned are restricted and (b) a lower non-formative region, composed exclusively of one type of cell destined to form the extra-embryonal ectoderm. This latter is in no sense to be regarded as a neo-formation, but is phylogenetically the equivalent of the extra-embryonal ectoderm in the Monotremata and Sauropsida as well as of the trophoblast (Hubrecht) or tropho-ectoderm (Hill) in the Monodelphia (Hill, 1910). In *Dasyurus* we have shown (Hill, *loc. cit.*) that the future formative and non-formative cell-categories become established as the outcome of the fourth cleavage-division which is unequal and qualitative, whilst in *Didelphys* it would seem that it is actually the first cleavage which is the differential division, one of the two blastomeres being formative in destiny, the other non-formative (Hartman, 1916; Hill, 1918). And there can be little doubt but that this precocious segregation (as Jenkinson, 1906, termed it) of the parent-cells of the tropho-ectoderm to form an independent entity, distinct from the parent-cells of the embryonal ectoderm (and the endoderm) is of the nature of a developmental adaptation of high functional significance which has arisen in response to the altered conditions resulting from that momentous event in the evolution of the Mammalia, the transition from oviparity to viviparity (Jenkinson, 1906; Hill, 1910). It involves an evident abbreviation in the ontogenetic process which we may suppose is conditioned by a more complete pre-determination in the egg.

In the Monodelphian Mammals we see the culmination of this same developmental adaptation, since in all of them, without exception, so far as we are aware, and in spite of even major variations in the details of the earlier stages of development, a blastocyst is sooner or later established, the wall of which is formed of a single layer of cells, regarded by the majority of embryologists as tropho-ectodermal or trophoblastic in significance, inside which the formative cells (embryonal ectoderm and endoderm) lie enclosed. This is the condition to which Selenka (1900) applied the term "Entypy" (Entypie des Keimfeldes) (*cf.* Hill, 1910, pp. 111, *et seq.*). It is distinctive of the Monodelphia as a group, though there would seem to be a few forms in which the separation of the cleavage-cells into two sharply defined categories, formative and trophoblastic, is only belatedly achieved.

In this connection there are two recent papers to which we may be permitted to refer.

The most remarkable example of delayed attainment of the entypic condition



known to us is furnished by the Elephant Shrew, *Elephantulus*, the early development of which has recently been described by C. J. van der Horst (1942). We give here a résumé of his observations which are based on an adequate material and are of very great interest. Some 60 or more eggs are ovulated from each ovary (van der Horst and Gillman, 1940), but of that huge number, only the one which first reaches the implantation site in the uterine horn will develop beyond the four-celled stage. The zona and corona radiata cells are thrown off at the time of ovulation or shortly thereafter, the tubal ovum being quite naked. In this respect *Elephantulus* appears to be unique.

The four spheroidal cells of the four-celled stage, instead of dividing to form a solid morula as is usual in the Monodelphia, flatten out and join up by their margins, so as to enclose the space which has already appeared between them, and so there arises a fluid-filled "blastula," with a complete wall formed of only four cells. In this condition, the one fortunate blastula reaches the implantation site and continues its development. The four cells divide and the blastula increases in size. When about 120 nuclei can be counted in its unilaminar and now very thin wall, two varieties of cell become recognizable in it, flattened cells with oval nuclei and cells of more rounded form with spherical nuclei. These latter cells project inwards and, according to the author, "are clearly in process of detaching themselves from the wall" (p. 61). They are capable of sending out pseudopodial processes by means of which they are connected with each other as well as with the flat cells of the wall (figs. 13-16). The author remarks that it is possible, though not likely, that some of the cells migrate inwards, assuming a more spherical form in so doing, but he regards it as more likely that cells acquire the internal position as the result of cell-division in planes tangential to the surface, and he emphasizes the fact that "this proliferation of cells" inwards occurs over the entire extent of the wall. The "amoeboid cells with their long pseudopodia," so produced, migrate inwards and, becoming connected by their processes, largely occupy the cavity of the blastula in the form of a loose cell-network (figs. 16 & 17). Then a process of concentration sets in and the network becomes converted into a compact cell-mass (figs. 18 & 19), the "embryonic knot" of the author, composed exclusively of prospective ectodermal cells.

The endoderm is formed in exactly the same way as the ectoderm. Amoeboid cells detach themselves from the wall of blastocyst and at first form a "wide-meshed reticulum" inside the latter. Later the cells flatten out and become applied to the surface of the "embryonic knot" now in the form of an amnio-embryonal vesicle, as well as to the inner surface of the wall of the blastocyst. They occur at first as isolated patches or as single cells (fig. 20), and out of these there is eventually formed a continuous layer of endoderm. The account of the formation of the endoderm is somewhat brief and no details of the relative size and cytological characters of the endoderm-cells are provided, nor is it stated whether or not it is possible to recognize them in the unilaminar wall, prior to their migration.\*

\* In a more recent paper (*S. Afr. J. Med. Sci.* 9 (1944), the author states that "during the formation of the (ectodermal) node [embryonic knot, future amnio-embryonal vesicle] it is not possible to discriminate between ectodermal and endodermal cells. They have a common origin from the amoeboid cells detached from the blastula wall as described before" (p. 32).

With the completion of the inward migration of the endoderm cells, the wall of the blastocyst becomes exclusively trophoblastic in constitution, and therewith the entypic condition becomes fully, if somewhat tardily, established.

In respect of its early development, *Elephantulus* clearly occupies a unique position among the Monodelphia, though if the conclusions of Blüntschi and Goetz are accepted as established, it is not alone in the substitution of a vesicular "blastula" for the usual solid morula, since the occurrence of such a stage had previously been recorded by these investigators in *Hemicentetes* (see below). Nevertheless, in spite of the fact that both these two Mammals are members of that basal but composite order, the Insectivora, and so may be regarded as lowly types, we should hesitate to regard the occurrence of this peculiar condition as a primitive developmental feature; and that is also the view of van der Horst (p. 64).

Confining our attention for the moment to *Elephantulus*, we may enquire what may have been the effect on the segmenting ovum of the shedding of the zona pellucida at the moment of ovulation or shortly after the same, a phenomenon clearly aberrant and secondary and doubtless to be associated with the unique and highly specialized structure the zona has acquired. Van der Horst and Gillman (1940) state that the zona "is not a thick homogeneous translucent membrane as in man and most mammals. Instead it seems to be irregularly divided by a strongly basophilic material into small non-staining compartments which correspond in size to the bordering cells of the corona radiata" (p. 74). Their figures (especially figs. 1, 7, 10, 15) show that it consists of a thicker inner layer investing the ovum, from which pass off what appear in section as very thin strands, more or less radial in disposition, which join an extremely thin outer layer, lying in intimate contact with the innermost cells of the corona radiata. These strands separate the "compartments" of the authors, which are occupied by a non-staining "gelatinous fluid." Immediately prior to ovulation, some of this fluid exudes on the free surface of the ovary through a slight break in the corona radiata and the overlying ovarian tissue (see figs. 7 & 20). The ovum may separate from the surrounding corona and zona at the time of ovulation or it may be discharged first, separation then taking place "in the periovarian space or when it arrives in the upper part of the tube" (p. 77).

We may well suppose that the absence of the zona has somehow or other so affected the blastomeres as to induce them to evolve some method whereby they can hang together, and that that need is a pressing one is borne out by van der Horst's observation that not only do the polar bodies frequently become free but "the blastomeres in the two- and four-celled stages may also become detached from each other" (p. 56). The method they seem to have discovered is that of flattening out and joining up by their margins (normally at the four-celled stage) so as to form a continuous layer enclosing a central cavity; and as indicative of how ingrained or impelling this need is, van der Horst states (p. 59 and fig. 9) that he has often observed that two detached cells of the four-celled stage are capable of giving origin to a small but complete blastula! Under these circumstances it would seem that the formation of a fluid-filled blastula with a pluri-potent wall has taken priority over the segregation of the trophoblast and formative cells. Nevertheless, the entypic condition is eventually realized and we are provided with a striking example of how environmental conditions can affect the course of development.



The formation of a transitory ectodermal cell-network in *Elephantulus* appears to be an absolutely unique phenomenon inside the Mammalia, but we are familiar with the occurrence of an endodermal cell-reticulum as a transitory developmental condition in the Monotremes and Marsupials, and such a condition has also been described in the Lemur, *Galago demidoffi*, by Gerard (1932) and by Hill (1938), and in the Musk-rat, *Crocidura*, by Sansom (1937).

Coming now to *Hemicentetes*, Blüntschli (1937, 1938), Blüntschli and Goetz (1937), and Goetz (1937, 1938), as indicated above, had already in 1937 stated that in this Insectivore, the morula stage is absent and is replaced by a hollow blastula. Unfortunately these observers had at their disposal only a limited amount of early material, so that their account of the early development is by no means complete.

According to Blüntschli (1937, p. 273), the number of ova shed from the ovaries is very large. In one uterine horn, up to 20 cleavage stages or young blastocysts may be found, but never more than 10 embryos (usually 6-8) are met with in the two horns, so that at best only one egg in four is destined to undergo normal development, the remainder degenerate.

The ovum is very small, about  $60\mu$  in diameter, and is enclosed in a very thin zona which, in striking contrast to that of *Elephantulus*, persists up to the time of attachment of the blastocyst to the uterine mucosa. Cleavage is not described, but it is said to result directly in the formation of a fluid-filled blastula of the same diameter as the ovum, the blastocoele of which is formed by the fusion of inter-cellular spaces which appear between the blastomeres soon after the first divisions. Its wall, of fairly uniform thickness, is unilaminar and composed of 16 cells. The cell-cytoplasm appears, from fig. 10 of Goetz (1938, p. 290), to be greatly vacuolated ("von schaumartiger Structur," Goetz) and strikes us as being cytologically in poor condition.

Both authors insist that the blastula exhibits a distinct polarity, though it is not always equally well marked. At one pole, the future embryonal pole, the nuclei are stated to be closer set and larger, and the cells a little smaller (with less protoplasm) than elsewhere. This important region of the wall is not figured unless the two bottom sections schematically figured in Goetz's Abb. 11 (1937, p. 291) pass through it, but it is nowhere so stated. Cell-division is said to proceed more actively at the embryonal pole than at the opposite pole, but no illustration of the blastula at this important stage is provided. As the outcome, the blastocyst becomes converted into a quite typical entypic blastocyst (Blüntschli, 1937, fig. 4, Goetz, 1938, fig. 2). It possesses a complete trophoblastic wall (composed, it is to be noted, of cells quite different in appearance from those forming the wall of the blastula) and at the embryonal pole, a small plano-convex mass of cells, the embryonal knot, which lies in close contact with the covering trophoblast. The latter, judging from the authors' account, would seem to arise in common with the formative cells of the knot, a mode of origin which is certainly not usual in the Monodelphia.

From now on, development proceeds along normal Monodelphian lines. In the following stage the blastocyst, now about  $120\mu$  in diameter, is implanted in the uterine mucosa by its embryonal pole and the zona has disappeared. From the embryonal knot there has been formed (a) a rounded mass of amnio-embryonal

ectoderm, a slight centrally situated intercellular space probably indicating the beginning of the primitive amniotic cavity, and (b) a small underlying endodermal yolk-sac vesicle. The endoderm, it is suggested, probably arises by delamination from the embryonal knot in the form of a solid mass which subsequently hollows out to form a small vesicle. This at first fails to reach the trophoblast, but it later expands and its endodermal wall forms a thin layer investing the free surface of the amnio-embryonal vesicle as well as the inner surface of the trophoblast (Blüntschi, 1938, figs. 3 & 4).

Such, in brief, is the extent of our knowledge of the early development of *Hemicentetes*. Apart from the blastula, the early development of this Insectivore exhibits no very exceptional features and proceeds along lines which can be paralleled more or less closely in other Monodelphia. The occurrence of a blastula-stage is thus all the more remarkable, and further details of its structure and of the frequency of its occurrence are necessary before its significance can be finally determined.

The question whether the method of endoderm-formation by the segregation of mother-cells endowed with the capacity for migration and possessed of definite prospective significance, which we now know holds good for the Ornithodelphia and the Didelphia, also occurs amongst the Monodelphia, can be answered affirmatively and without qualification for at least one member of that sub-class, the Armadillo (*Tatusia novemcincta*). In this form Patterson (1913) has shown that the embryonal knot of the early blastocyst is composed of two types of cell, larger, lighter staining prospective ectodermal cells and smaller, more deeply staining endodermal mother-cells. The latter migrate out from amongst the prospective ectodermal cells either directly or after division and collect on the under-surface of the knot to form at first a network and later a connected layer of endoderm, whilst the prospective ectodermal cells form a spherical mass, the just mentioned knot, which later hollows out to form an amnio-embryonal vesicle. But in various other Monodelphia the gradual appearance, during the growth of the blastocyst, of more or less isolated endodermal cells on the under-surface of the knot does seem to indicate that the same process of segregation is also operating in them, and the fact that the endodermal cells are capable of wandering out from below the knot to form an internal lining to the trophoblast is proof enough of their possession of migratory powers. In this connection the reader is referred to the account of Assheton (1894) of the first appearance and the peripheral spreading of the endoderm in the blastocyst of the Rabbit and the remarks of Hill thereon (1910, pp. 70–72).

Attention may also be called to the significant conclusion reached by Heuser and Streeter (1941) in their recent memoir on the early development of the rhesus monkey (*Macaca mulatta*), that the primitive endoderm cells which are already recognizable in the 8-day blastocyst, "are a direct product of the primary segregation and cleavage of the egg" (p. 37). This conclusion is further elucidated by the statement that "in the youngest ovum (C 614, pl. 1) a few primary endodermal cells, 7 in number, have moved out of the thickened (inner cell) mass and arranged themselves on its ventral or internal surface. It is possible that some of the small cells scattered throughout the inner cell mass are endoderm not yet migrated" (p. 35).



But on this question, it is clearly premature to generalize in the existing state of our knowledge, and all we can say is that in certain Monodelphia there is evidence pointing to the conclusion that in the mode of formation of their primary germ-layers they conform to the same determinate plan that we now know operates in the Ornithodelphia and the Didelphia, and that in particular the endoderm arises by the segregation of predetermined mother-cells, endowed with migratory properties.

#### D. THE ORIGIN OF THE PRIMARY GERM-LAYERS IN THE SAUROPSIDA.

Finally we may enquire in how far the process of germ-layer formation in the Sauropsida links up with or throws light upon the same process in the Ornithodelphia, at the outset no very hopeful task, since there is as yet no general agreement amongst investigators as to the details of the process in either the Reptiles or the Birds.

##### 1. *Reptiles.*

Prior to the appearance of the paper of Pasteels (1937) on the gastrulation process in the Tortoise, *Clemmys leprosa*, the view was generally held and is still maintained by Peter (1938) in his latest contribution, that in Reptiles the two primary layers are formed by a simple process of delamination, *i. e.* the superficial cleavage cells become arranged to form a connected layer of ectoderm, whilst the deeply seated cells give origin to the endoderm, which however varies considerably in the different species in the time of attainment of its completed condition as a continuous membrane (earliest in the Chameleon, later in the Lizard, still later in Snakes, and most belatedly of all in the Chelonia (Peter, 1938) and in the degree to which post-cleavage cells contribute to it (*cf.* Will, 1895).

Pasteels (*loc. cit.*), on the other hand, maintains, in opposition to all other investigators, that in the Tortoise, *Clemmys leprosa*, the primary endoderm is formed by invagination at the postero-lateral margin of the unilaminar embryonal shield area of the blastoderm well within its posterior rim.

In the earliest stage he describes (embryo 13), the blastoderm (fig. 1 B) consists of a superficial layer of flattened cells and an underlying single layer of more or less disconnected cells, of which some, of large size, show evident relations with the yolk. There is, as yet, no trace of the "primitive plate." In his next stage (embryo 14), the embryonal area of the blastoderm, owing to the continued spreading of the blastoderm, has become extremely thin (fig. 2) and consists of the superficial layer now composed of cubical cells with, below it, sparse, widely dispersed deep cells (fig. 3). In embryo 15, deep cells are rare and limited to some large yolk-cells. The author accordingly claims to have demonstrated, on the evidence provided by these two embryos, that during its progressive spreading the embryonal area of the blastoderm becomes converted into a unilaminar layer as the result of the intercalation of the deep cells into the original superficial layer, in much the same way as happens during the formation of the unilaminar blastoderm in the Monotreme. Peter (*loc. cit.*) points out that in no other Reptile has such a unilaminar stage been recorded.

In the author's next stage (embryo 16), the sub-germinal cavity has appeared and the embryonal shield has become visibly delimited. Below the superficial layer there are now present numbers of deep cells (fig. 4). These, the author

believes, are endodermal cells which have been invaginated in the region of a thickening of the superficial layer which has been formed at the margin of the embryonal shield (fig. 4 a). This "blastoporic thickening" occupies, according to the author, not only the posterior but also the postero-lateral margins of the embryonal shield and corresponds to the "Randsichel" described by Ballowitz (1901) in *Tropidonotus*. Later, as the result of a cellular movement of concentration towards the middle line, this thickening becomes transformed into the rounded "blastoporal plate" (primitive plate of authors), and a blastoporic groove appears on its surface. Still later (embryo 27), the invagination of the endoderm gives place, "sans transition aucune" (p. 126), to that of the "prolongement céphalique," the head-process or chorda-mesoderm process, with its canal opening on the surface of the primitive plate by the blastopore.

Such in outline is Pasteels' account of the formation of the endoderm by invagination in *Clemmys*. The occurrence of such a process in a Reptile, if confirmed, is clearly a discovery of great interest and importance, since it would enable us to connect up the early ontogenetic processes in the Anamnia and the Amniota, as Pasteels claims to have succeeded in doing also for the later stages. But it seems to us that certain of his observations require further elucidation and illustration (notably his description of the attainment by the embryonal area of the unilaminar condition, nothing being said as to the conditions obtaining in the rest of the blastoderm and his account of the first appearance of the endoderm) before his results can be regarded as fully established.

Peter (1938), indeed, after a renewed study of endoderm-formation in the Chameleon, Lizard and Snakes, wholly rejects Pasteels' interpretation and re-affirms his conviction that in the forms mentioned, and probably also in Chelonia, the endoderm arises by delamination and not through any process of invagination and has no, or at most only insignificant connection with the primitive plate. An origin of the entire endoderm from this source is, he says, "völlig zuruckzuweisen" (p. 530). On this view, there is no question of the inwandering of cells either by invagination or migration. The endoderm arises *in situ* and the prospective value of the cleavage cells would seem to be simply a function of their position.

These, then, are the two opposing views as to the origin of the endoderm in the Reptilia, and it will be evident that they are quite irreconcilable, the one with the other.

We agree with Pasteels (*loc. cit.*, p. 114) that in the Chordata, invagination is a more primitive method of endoderm-formation than delamination. The latter appears to be a purely non-determinate process, incapable of being linked up with the determinate Anamniotic mode of endoderm-formation by invagination, on the one hand, or with the determinate Mammalian type, involving the active inward migration of predeterminate cells, on the other. But we must continue to reckon with its occurrence in the Reptilia until such time as the conclusions of Peter are shown to be untenable, even if we are in accord with Pasteels when he writes (*loc. cit.*, p. 114) "il semble vraiment incompréhensible que l'on doive admettre que l'entoblaste se forme chez des Amniotes inférieurs tels que les Reptiles, par délamination."

It may be asked, supposing delamination were disposed of, and the occurrence of invagination established, how would the latter help us to bridge the gap between



the Reptile and the Mammal? That question seems to present no very serious difficulty to Pasteels or to Dalcq (1938). On the basis of Merbach's observations on the Fowl (*v. p.* p. 129) and the observations of Hill (1910) and Kerr (1934) on Marsupials, Pasteels has coined the hybrid, and in our opinion, singularly inappropriate term, "poly-invagination" to designate the type of endoderm-formation, involving the diffuse inward migration of predetermined cells, which occurs in the latter and also, as we now know, in the Monotremes, and which Merbach avers also occurs in the blastoderm of the Fowl and at the same time to indicate that he regards the process in question as simply a modification of the normal process of invagination. He writes (*loc. cit.* p. 114), "Si ce mode d'invagination est évidemment très différent de l'invagination massive et localisée des Amniotes, elle est cependant en tant qu'*invagination* un processus plus primitif que la délamination." Dalcq (1938) finds Pasteels' account of the origin of the endoderm by invagination in *Clemmys* "extremely convincing" (p. 13) and adopts his term "poly-invagination." He also accepts Pasteels's confirmation of Merbach's account of the formation of the endoderm in the Fowl (*v. p.* p. 129) and remarks thereanent "the process [of poly-invagination] is most active in the dorsal half of the disc. *It is similar to that of Reptiles* but scattered over a larger territory" (p. 14, italics ours). We think, however, that Pasteels is nearer the mark when he admits that the two processes are very different. In the one case (Reptile, according to Pasteels), we have to do with a migratory movement *en masse*, *i. e.* an invagination of prospective endodermal cells, all presumably located in one site, viz. the primitive plate or its forerunner, whereas in the other (Monotremes, Marsupials and Birds), the prospective endodermal cells have become distributed throughout the extent of the blastoderm, and we have to do with a diffuse migration inwards of the individual cells. It is a method which ensures the early establishment of the endoderm as a continuous layer, well prior to the appearance of the mesoderm; and even if we admit that it has been derived from, or has replaced, the ancestral invagination method, that is no justification for terming it "poly-invagination."

## 2. *Birds.* (By J. H. Woodger and J. P. Hill).\*

Although it is a far cry, phylogenetically, from the Birds to the Monotremes, a brief survey of our present knowledge of their early development may not be so devoid of interest in the present connection, as it appears to be at first sight, if we call to mind how the Birds have paralleled the Mammals in the evolution of a completely 4-chambered heart, a high body-temperature, with an associated insulating body-covering, and an elongated primitive streak and all that that implies, parallelisms to which one of us (H.) had long been accustomed to refer in his teaching and on two of which (body-temperature and primitive streak) Pasteels has recently commented (1937 *b*, pp. 480-482).

The contention of Patterson (1909) that in the Pigeon the endoderm is formed by a process of invagination at the posterior margin of the blastoderm, would appear to be no longer tenable in face of the adverse criticisms of, amongst others, Assheton (1912), Pasteels (1937) and Peter (1938).

Two other views remain: (1) the view held by many of the older observers, and strongly supported in recent times by Peter (1938), that the endoderm in

\* Included here with the consent of Dr. Woodger.

the Fowl and Pigeon is formed not through the inwandering of cells but by a process of delamination as in Reptiles, *i. e.* the undifferentiated layer, two or more cells in thickness, which constitutes the early blastoderm, splits apart *in loco* into superficial and deep layers as the result of the appearance in it of small spaces or clefts which gradually run together to form a continuous fissure separating the two layers; (2) the more recent view according to which the endoderm is formed as the result of an inward proliferation and "invagination" of cells, a process envisaged by Gräper (1937) as "gastrulation durch multiple Invagination," regarded by Merbach (1935) as being effected through a "diffuse Urmund" and termed by Pasteels (1937) "Polyinvagination," theoretical conceptions which only serve to obscure the question at issue. We may well ask how can a blastopore be diffuse and how can individual cells invaginate? (*cf.* Peter, 1938, p. 412).

The paper of Merbach (1935) we find quite inconclusive, based as it is on a study of blastoderms exhibiting numerous folds of varying depth which, as Peter (1938) has conclusively demonstrated and as is obvious to anyone familiar with well-fixed avian blastoderms, are none other than gross artefacts; moreover, the really critical figures which purport to provide evidence in support of the contentions of the writer completely fail to do so. On the other hand, it should be stated that Pasteels (1937, p. 393) finds the paper "très convaincant"! Merbach's conclusions, in brief, are to the effect that in non-incubated and quite shortly incubated blastoderms of the fowl, a cell-movement (involving proliferation and invagination) from the upper layer into the forming lower layer occurs, especially from the sides and the bottom of the folds which have arisen in the upper layer and in the angles where the folds join the surface. In addition, proliferation also occurs in the small areas where the upper and lower layers are connected. During this process the blastoderm is said to become reduced in area (as we should expect from the folding of the superficial layer). The deep cells so originating are distinguishable from those of the latter layer by their richer content of yolk-granules.

The folds for Merbach represent a "diffuse blastopore" by means of which the endodermal cells invaginate. Merbach also regards it as possible that an inwandering of cell-material occurs round the posterior edge of the blastoderm (which would thus form an additional part of the "diffuse blastopore"), as advocated by Patterson, but states this is only of slight importance, at least in the Fowl.

Pasteels (1937) was unable to find any experimental evidence in support of the occurrence of invagination at the posterior margin of the blastoderm, but he states that otherwise he is able to confirm the findings of Merbach. This, however, is only partially true. What he does confirm is (1) that the endodermal cells are recognizable at the moment of "invagination" or after the same by the fact that their yolk-granules stain deeply with iron-haematoxylin, whilst those in the superficial cells remain pale, and (2) that there is evidence of the "invagination" of the deeply staining cells. He points out that in his fig. 4, p. 399, it can be seen that the deep cells are strongly stained, that small groups of similarly stained cells occur in the superficial layer, and that near the centre of the figure there is present a single, pyriform, deeply stained cell in process of "invagination." He accordingly claims that the cells of the deep layer of the blastoderm are distinguishable by their staining reactions even before their "invagination," and



he concludes that "l'entoblast, tout choses étant égales, se forme de la même façon chez les Oiseaux et les Marsupiaux" (p. 399).

Pasteels' observations are suggestive enough, so far as they go, but they can hardly be regarded as furnishing conclusive proof that the whole of the endoderm arises by the "invagination" of deeply staining cells from the superficial layer of the blastoderm. Even Peter (1938, p. 390) admits that in his most advanced blastoderm from the new-laid egg (Nr. 138), as well as in those incubated for a few hours, a few places can be found in his zone 3 (an area where only sparse endoderm cells are present) in which there is evidence that cells separate out from the superficial layer to become added to the endoderm. He illustrates such a place in his fig. 13 (p. 390) and describes it as consisting of a group of large, rounded, clear cells with large nuclei (said to be pale but not so shown in the figure) which, owing to their greater breadth and length, project down below the under-surface of the surrounding ectoderm composed of close-set columnar cells. These large cells are in the closest connection with more deeply situated cells which have exactly the same appearance, and these in their turn resemble the neighbouring endodermal cells already separated. He goes on to say "es besteht wohl kein Zweifel, dass es sich hier um Ablösung von Zellen des inneren Keimblattes von der dann zum Ektoderm werdenden oberen Schicht handelt" (p. 390-391). Nevertheless, the occurrence of such areas in no way weakens his belief in the origin of the endoderm by delamination, and he makes no attempt to account for them, apart from remarking that mature endoderm cells can hardly be supposed to have wandered into the ectoderm! But advocates of the migration view will doubtless draw their own conclusions.

We, ourselves, have some additional evidence to offer bearing on the question at issue, since we have before us a record of observations on the early development of the Sparrow (*Passer domesticus*) made prior to 1925, on an adequate and well-fixed material and hitherto unpublished (apart from a brief notice of a demonstration in Bio-Morph. i. p. 326, 1938). More recently we have confirmed and extended these observations. They led us to the conclusion that in this bird the formation of the germ-layers is effected by a combination of two processes which we designated in our original notes as segregation and delamination, the former process preceding and accompanying the latter and involving the migratory movement of pre-determined cells; and that conclusion we are still prepared to maintain. But in continuing to use the term "delamination," we would emphasize at the outset that the separation into layers, which the term implies, is no mere passive happening but is initiated by an active process of cellular differentiation affecting in the first instance the cells destined to form the future ectoderm and only later those destined to form the endoderm.

The Sparrow has this advantage over the Pigeon and Fowl, that germ-layer formation begins only after the egg is laid. The blastodisc in the recently laid egg appears as a circular biconvex mass of compactly arranged cells, measuring about 1.40 mm. in diameter and about 0.12 mm. in maximum thickness. Centrally it is 3-4 cells in depth and peripherally thins out to a thickness of 1-2 cells. It rests directly on the white yolk-bed, no sub-germinal cavity being present.

As incubation proceeds, the blastodisc increases in surface-extent, and when it has attained a diameter of about 1.7 mm. and is some 5-6 cells in thickness,

the first trace of the sub-germinal cavity appears in the form of a narrow cleft situated between the central region of the disc and the yolk-bed. This cleft gradually increases in extent and in depth as development proceeds, and so comes to form a well-marked continuous fluid-filled cavity.

The blastodisc, as it expands, thins out somewhat over its central region and appears as a fairly uniform layer, about 4 cells in thickness. Outside the limits of the sub-germinal cavity, where it rests directly on the peripheral white yolk, it is somewhat thicker, and beyond that it thins out to the thickness of a single cell.

In the disc (Pl. XXVII, fig. 176), two types of cell are distinguishable, viz. (a) large cells, the cytoplasm of which is crowded with small deeply staining eosinophil yolk-spheres. Such cells are mainly located in the deep part of the disc, and here they often appear oval or rounded in form, but they also occur at and below its upper surface; (b) smaller, less deeply staining cells, with less numerous and much finer pale staining yolk-granules; these cells are mainly disposed at and below the upper surface of the disc. Type (a) we regard as prospective endodermal cells and type (b) as prospective ectodermal.

The first readily detectable sign of the commencing differentiation of the germ-layers becomes apparent when the blastoderm has reached a diameter of from about 2 to 2.5 mm. Over its central region, overlying the sub-germinal cavity, the prospective ectodermal cells which, in the meantime, would seem to have largely become segregated at the surface, begin to take on an epithelial arrangement. This process of epithelial formation does not proceed uniformly and continuously over the extent of the central area but occurs in patches of varying extent, being most rapidly effected in those areas in which included yolk-rich cells are less numerous. In this way a superficial epithelial layer, destined to form the ectoderm and at first discontinuous, becomes established (Pl. XXVII, figs. 177 & 178).

It is composed of light-staining yolk-poor cells, cubical and columnar in form, intermingled with much less numerous yolk-rich cells, and is clearly distinguishable from the underlying loose, irregular lower layer, 2-3 cells in thickness, formed mainly of large yolk-rich cells and destined to form the endoderm. The distinction between the two layers is still further enhanced by the appearance of horizontally disposed cleft-like spaces between the two, as the outcome of the differentiation of the ectoderm and which, like the latter, are at first discontinuous. In the portions of the blastoderm situated between these clefts, yolk-rich cells, both superficial and deep, tend to be more numerous than elsewhere, and as a consequence the differentiation of the ectoderm is retarded. Careful study of the sections reveals that in such places an inward migration of the more superficially situated yolk-rich cells is taking place, and it is noteworthy that, where this migratory movement is markedly in evidence, the differentiating surface-layer often appears slightly grooved (Pl. XXVII, fig. 178). A similar inward migration of individual yolk-rich cells can also be observed in areas where the superficial layer has been definitely established (Pl. XXVII, fig. 177).

Furthermore, if we are correct in identifying the yolk-poor cells in the undifferentiated blastoderm as prospective ectodermal, it is evident that those of them that are more or less deeply situated must be capable of migrating to the surface,



and of this we have definite evidence in the blastoderm at the stage when the differentiation of the ectoderm is just beginning. It doubtless occurs also in still earlier stages but it is much more difficult to detect.

The observations briefly set forth above suffice to show that the establishment of the germ-layers in the Sparrow is not effected by a seemingly simple and passive process of separation or splitting apart of the constituent cells of an undifferentiated blastoderm into upper and lower layers; *i. e.* by a process of delamination as envisaged by Peter (*loc. cit.*) in the Fowl and Pigeon. In his own words ((1), p. 382), "Das innere Keimblatt entsteht also nicht durch Einwandern von Zellen, sondern in loco durch Abspaltung von einer einheitlichen undifferenzierten Zellmasse."

We hold, on the contrary, that it is the outcome of two combined and essentially active processes, segregation and delamination. Segregation involves the migratory movement of prospectively determined cells into their definitive positions, the deeply seated prospective ectodermal cells migrating outwards into the surface-layer and the superficially situated prospective endodermal cells migrating inwards into the lower layer. Delamination, the actual separation of the blastoderm into upper and lower layers, is effected by a process of differentiation which involves alterations in the form and arrangement of the cells and results first in the establishment of a continuous epithelial layer at the surface, the future ectoderm, composed of yolk-poor cells. It is sharply marked off, by its epithelial character and the now continuous cleft-like space, from the underlying deeper portion of the blastoderm, forming the lower layer, composed of yolk-rich cells, 2-3 cells in thickness, which is destined to become transformed later on into a continuous epithelial membrane, the future endoderm.

We thus find ourselves in agreement with Merbach and Pasteels, so far as concerns the occurrence of an inward migratory movement on the part of superficially situated prospective endodermal cells, but we differ from Pasteels in holding that in the Sparrow only a part of the prospective endodermal cells is involved in this movement, the remainder and larger part of the endoderm being furnished by the yolk-rich cells located in the deep portion of the blastoderm, *i. e.* in the future lower layer.

Finally, on the evidence now available, we are able to extend the contention of Pasteels (*ante*, p. 130) and to advance the conclusion that the Birds exhibit, in the formation of their primary germ-layers, the same determinate type of development as is seen in the Monotremes and Marsupials. If this conclusion is accepted a fresh incentive is provided for a renewed and intensive study of germ-layer formation in the Reptiles.

#### LITERATURE CITED.

- AGASSIZ, L., & CLARK, H. J. (1857). *Contributions to the natural history of the United States of America.—2. Embryology of the turtle.* Boston.
- AGASSIZ, A., & WHITMAN, C. O. (1884). On the development of some pelagic fish eggs. Prel. Notice, *Proc. Amer. Acad. Arts Sci.* 20, 23.
- ASSHETON, R. (1894). A re-investigation into the early stages of the development of the rabbit. *Quart. J. micr. Sci.* n.s. 37, 113.
- ASSHETON, R. (1910). *Tropidonotus* and the "archenteric knot" of *Ornithorhynchus*. *Quart. J. micr. Sci.* n.s. 54, 631.

- ASSHETON, R. (1912). Gastrulation in birds. *Quart. J. micr. Sci.* n.s. **58**, 145.
- BALFOUR, F. M. (1881). *A treatise on comparative embryology*.—2, 132–34. Macmillan & Co.: London.
- BALLOWITZ, E. (1901). Die Gastrulation der Ringelnatter. *Z. wiss. Zool.* **70**, 675.
- BLOUNT, MARY. (1907). The early development of the pigeon's egg, with special reference to the supernumerary sperm nuclei, etc. *Biol. Bull.* **13**, 231.
- BLÜNTSCHLI, H. (1937). Die Frühentwicklung eines Centetinen (*Hemicentetes semispinosus* Cuv.). *Rev. suisse Zool.* **44**, 271.
- BLÜNTSCHLI, H. (1938). Le développement primaire et l'implantation chez un centetiné (*Hemicentetes*). *C.R. Ass. Anat.* **1938**, 1. Bâle.
- BLÜNTSCHLI, H., & GOETZ, R. H. (1937). Le développement primaire et la formation d'un placenta perforé très compliqué et du type labyrinthe chez *Hemicentetes*. *Bull. Acad. Malgache*, n.s. **20**, 73.
- BOYD, M. M. M. (1942). The oviduct, foetal membranes and placentation in *Hoplodactylus maculatus* Gray. *Proc. zool. Soc. Lond. A*, **112**, 65.
- DALCQ, A. M. (1938). *Form and causality in early development*. Cambridge University Press.
- DUVAL, M. (1884). De la Formation du Blastoderme dans l'oeuf d'Oiseau. *Ann. Sci. nat.* Ser. 6, **18**, 1.
- FLYNN, T. T., & HILL, J. P. (1939). The development of the Monotremata.—Part IV. Growth of the ovarian ovum, maturation, fertilization and early cleavage. *Trans. zool. Soc. Lond.* **24**, 445.
- FLYNN, T. T., & HILL, J. P. (1941). The later stages of cleavage and the formation of the primary germ-layers in the Monotremata. (Preliminary Communication). *Proc. zool. Soc. Lond. A*, **113**, 233.
- GATENBY, J. B., & HILL, J. P. (1924). On an ovum of *Ornithorhynchus* exhibiting polar bodies and polyspermy. *Quart. J. micr. Sci.* **68**, 229.
- GERARD, P. (1932). Etudes sur l'ovogenèse et l'ontogenèse chez les Lémuriens du genre Galago. *Arch. Biol.* **43**, 93.
- GOETTE, A. (1874). Beiträge zur Entwicklungsgeschichte der Wirbelthiere.—II. Die Bildung der Keimblätter und des Blutes in Hühnerei. *Arch. mikr. Anat.* **10**, 145.
- GOETZ, R. H. (1937). Studien zur Placentation der Centetiden.—II. *Z. Anat. EntwGesch.* **107**, 274.
- GOETZ, R. H. (1938). On the early development of the Tenrecoidea. *Bio-morph.* **1**, 67.
- GRÄPER, L. (1937). Die Gastrulation nach Zeitaufnahmen linear markierter Hühnerkeime. *Anat. Anz. (Ergänzhft.)*, **83**, 6.
- HARTMAN, C. G. (1916, 1919). Studies in the development of the opossum, *Didelphys virginiana* L. *J. Morph.* **27**, 1, & **32**, 1.
- HEUSER, C. H., & STREETER, G. L. (1941). Development of the Macaque embryo. *Contr. Embryol. Carneg. Instn.* **29**.
- HILL, C. J. (1941). The development of the Monotremata.—Part V. Further observations on the histology and secretory activities of the oviduct prior to and during gestation. *Trans. zool. Soc. Lond.* **25**, 1.
- HILL, J. P. (1910). The early development of the Marsupialia with special reference to the native cat (*Dasyurus viverrinus*). *Quart. J. micr. Sci.* **56**, 1.
- HILL, J. P. (1918). Some observations on the early development of *Didelphys aurita*. *Quart. J. micr. Sci.* **63**, 91.
- HILL, J. P. (1933). The development of the Monotremata.—Part II. The structure of the egg-shell. *Trans. zool. Soc. Lond.* **21**, 443.
- HILL, J. P. (1938). Implantation of the blastocyst in *Galago demidoffi* (Demonstration). *Bio-morph.* **1**, 333.
- HILL, J. P., & MARTIN, C. J. (1894). On a Platypus embryo from the intra-uterine egg. *Proc. Linn. Soc. N.S.W.* 2nd ser. **10**, 43.



- HILL, J. P., & WOODGER, J. H. (1938). The origin of the endoderm in the sparrow. *Bio-morph.* 1, 326.
- HIS, W. (1868). *Untersuchungen über die erste Anlage des Wirbelthierleibes. Die erste Entwicklung des Hühnchens im Ei.* Leipzig.
- HORST, C. J. VAN DER. (1942). Early stages in the embryonic development of *Elephantulus*. *S. Afr. J. Med. Sci.* 7, 55, Biol. Suppl.
- HORST, C. J. VAN DER. (1944). Further stages in the embryonic development of *Elephantulus*. *Ibid.* 9, 29, Biol. Suppl.
- HORST, C. J. VAN DER, & GILLMAN, J. (1940). Ovulation and corpus luteum formation in *Elephantulus*. *Ibid.* 5, 73.
- HRABOWSKI, H. (1926). Das Dotterorgan der Eidechsen. *Z. wiss. Zool.* 128, 305.
- JENKINSON, J. W. (1906). Remarks on the germinal layers of Vertebrates and the significance of the germinal layers in general. *Mem. Manch. lit. phil. Soc.* 50, Mem. No. 3.
- KERR, T. (1934). Notes on the development of the germ-layers in Diprotodont Marsupials. *Quart. J. micr. Sci.* 77, 305.
- KÖLLIKER, A. (1875). Zur Entwicklung der Keimblätter im Hühnerei. *Verh. phys.-med. Ges. Würzburg*, n.f. 8, 13.
- MERBACH, H. (1935). Beobachtungen an der Keimscheibe des Hühnchens vor dem Erscheinen des Primitivstreifens. *Z. Anat. EntwGesch.* 104, 635.
- PASTEELS, J. (1937). Etudes sur la gastrulation des Vertébrés meroblastiques.—II. Reptiles. III. Oiseaux. IV. Conclusions générales. *Arch. Biol.* 48, 105; 381.
- PATTERSON, J. T. (1909). Gastrulation in the pigeon's egg. *J. Morph.* 20, 65.
- PATTERSON, J. T. (1913). Polyembryonic development in *Tatusia novemcincta*. *J. Morph.* 24, 559.
- PETER, K. (1934). Die erste Entwicklung des Chamäleons (*Chamaeleo vulgaris*) verglichen mit der Eidechse (Ei, Keimbildung, Furchung, Entodermbildung). *Z. Anat. EntwGesch.* 103, 147.
- PETER, K. (1935). Die innere Entwicklung des Chamäleonkeimes nach der Furchung bis zum Durchbruch des Urdarms. *Z. Anat. EntwGesch.* 104, 1.
- PETER, K. (1938). Untersuchungen über die Entwicklung des Dotterentoderms.—1. beim Hühnchen, 2. bei der Taube, 3. bei Reptilien. *Z. mikr.-anat. Forsch.* 43, 362 & 44, 498.
- RÜCKERT, J. (1885). Zur Keimblattbildung bei Selachiern. *S.B. Ges. Morph. Physiol. München.* 1, 47.
- SANSOM, G. S. (1937). The placentation of the Indian musk-shrew (*Crocidura caerulea*). *Trans. zool. Soc. Lond.* 23, 267.
- SELENKA, E. (1900). *Studien über Entwicklungsgeschichte der Tiere.* Pt. 8. Wiesbaden: C. W. Kreidel.
- SEMON, R. (1894). Zur Entwicklungsgeschichte der Monotremen. *Zool. Forsch. in Australien*, 2, 59. Jena: G. Fischer.
- VIRCHOW, H. (1892 a). Das Dotterorgan der Wirbeltiere. *Z. wiss. Zool.* 53. Suppl. 161.
- VIRCHOW, H. (1892 b). Das Dotterorgan der Wirbeltiere (Fortsetzung). *Arch. mikr. Anat.* 40, 39.
- WILL, L. (1895). Die Anlage der Keimblätter bei der Eidechse (*Lacerta*). *Zool. Jb. Anat.* 9, 1.
- WILSON, J. T., & HILL, J. P. (1907). Observations on the development of *Ornithorhynchus*. *Philos. Trans. B*, 199, 31.
- WILSON, J. T., & HILL, J. P. (1915). The embryonic area and so-called "primitive knot" in the early Monotreme egg. *Quart. J. micr. Sci.* 61, 15.

## LIST OF COMMON REFERENCE LETTERS ON THE PLATES.

<i>cre.</i> Cytoplasmic reticulum of yolk-bed.	<i>pr.end.</i> Primitive endoderm cell.
<i>dgc.</i> Degenerate cell.	<i>pr.end.d.</i> Deep primitive endoderm cell.
<i>dpc.</i> Deep disc-cell.	<i>sc.</i> Sister-cell.
<i>ect.</i> Ectoderm (cell).	<i>sdc.</i> Sub-disc cell.
<i>emc.</i> Endodermal mother-cell.	<i>sgc.</i> Sub-germinal cavity.
<i>end.</i> Endoderm (cell).	<i>sh.</i> Shell.
<i>gp.</i> Gap in yolk-membrane.	<i>smc.</i> Sub-marginal cell.
<i>gr.</i> Germ-ring.	<i>smv.</i> Sub-marginal vitellocyte.
<i>mbi.</i> Marginal region of blastoderm.	<i>ybc.</i> Yolk-bed cell.
<i>mc.</i> Marginal cell.	<i>ybl.</i> Yolk-ball.
<i>pdc.</i> Peripheral disc-cell.	<i>ybn.</i> Yolk-bed nucleus.
<i>pr.</i> Process of primitive endoderm cell.	<i>ym.</i> Yolk-membrane.
<i>pv.</i> Peripheral vitellocyte.	<i>za.</i> Zona-albumen layer.
<i>p.ect.</i> Prospective ectoderm cell.	



## EXPLANATION OF THE PLATES.

## PLATE I.

## LC 1 (E.1.8.30).

- Fig. 1. Section (4-2-2) through the blastodisc, passing just to one side of its centre. *mc.*, marginal cell. *pd.*, peripheral disc-cell. See text, p. 8). ( $\times 170$ .)
- Fig. 2. Central portion of a more peripheral section (7-1-2) through the disc. See text, p. 8. ( $\times 300$ .)
- Fig. 3. Periphery of section (2-1-2) showing a central disc-cell (*c.* 2) and the division of a marginal cell (not yet completed) into a central cell (*cc.*) and a peripheral cell (*pd.*). ( $\times 315$ .)
- Fig. 4. An isolated vitellocyte in section (1-5-2). ( $\times 795$ .)
- Figs. 5 *a*, 5 *b* & 5 *c*. From three consecutive sections (4, 5 and 6-4-2) to illustrate the origin of a vitellocyte (*pv.*) from a marginal cell (*mc.*). See text, p. 10. ( $\times 425$ .)

## LC 2 (J.15.8.30).

- Figs. 6 & 7. Sections through the central region of the disc (3-2-2 and 6-2-2). *pd.*, peripheral disc-cell. *pv.*, peripheral vitellocyte. See text, p. 12. ( $\times 176$ .)
- Fig. 8. Higher power view of the central area of fig. 7. See text, p. 12. ( $\times 328$ .)

## PLATE II.

## LC 2 (J.15.8.30).

- Fig. 9. Section (8-2-2) through the central region of the disc. *pd.*, peripheral disc-cell. See text, p. 12. ( $\times 166$ .)
- Fig. 10. Higher power view of the right marginal region of fig. 9. ( $\times 308$ .)
- Fig. 11. Tangential section (6-4-2) showing two marginal cells in division. ( $\times 212$ .)
- Figs. 12 *a*, 12 *b*, 12 *c*, 12 *d*. Four sections (2 and 1-4-1, and 8 and 6-3-1) to show the origin of a daughter-vitellocyte (*pv.*1) from a parent vitellocyte (*pv.*). *pd.*, peripheral disc-cell. See text, p. 14. ( $\times 305$ .)

## LC 3 (VVH 21).

- Fig. 13. Surface view of blastodisc. Diameter (including the ring of vitellocytes), as measured in the entire egg,  $0.88 \times 0.78$  mm. ( $\times$  about 55.)
- Fig. 14. Section (4-4-8) through the disc, just to one side of its centre. *dpc.*, deep cell. *pd.*, peripheral disc-cell. ( $\times 243$ .)
- Fig. 15. Section (2-1-9) through the disc, the seventh to one side of fig. 14. See text, pp. 15-16. ( $\times 243$ .)

## PLATE III.

## LC 3 (VVH 21).

- Fig. 16. Portion of section (1-1-8) showing two vitellocytes (*pv.*) with their processes and the delicate cytoplasmic reticulum in the yolk. ( $\times 562$ .)
- Fig. 17. Section (1-3-8) passing through the periphery of a vitellocyte (*pv.*) and showing on the left its processes anastomosing to form a network (*pvn.*) with fine yolk-granules in its strands and, below and on the right, the delicate cytoplasmic reticulum (*cre.*) in the yolk with which it is continuous. ( $\times 1020$ .)

## LC 4 (B.1.8.30).

- Fig. 18. Section (5-3-2) passing through the centre of the disc. *sdc.*, sub-disc cell. See text, p. 17. ( $\times 385$ .)
- Fig. 19. Section (9-3-2) through the disc (the fourth to one side of fig. 18) and including the peripheral cell (*pd.*) on the left. See text, p. 17. ( $\times 300$ .)
- Fig. 20. Section (2 and 3-4-2) showing the marginal region of the disc, with the peripheral cell (*pd.*) on the right. ( $\times 377$ .)

## LC 5 (A.15.7.30).

- Fig. 21. Section (1-2-2) passing through the centre of the disc, its central region being clearly delimited below from the underlying vacuolated central core of the yolk-bed. Immediately to the left of the core is a deep sub-disc cell (*sdc.* 5). See text, p. 21. ( $\times 308$ .)

## PLATE IV.

## LC 5 (A.15.7.30).

- Fig. 22. Section (7-1-2) through the disc (the third to one side of fig. 21). The delimitation of the disc from the yolk-bed is indicated only over a limited area on the right side of the figure. *c.*, deeply seated peripheral cell. *sdc.* 3, sub-disc cell. *sdc.* 4, deep sub-disc cell. ( $\times 380$ .)
- Fig. 23. Section (3-1-2) through the disc (the fourth peripherally to fig. 22), especially to show the relations of the sub-disc cells, *sdc.* 1 and *sdc.* 2, to the disc-cells proper and the deep sub-disc cell (*sdc.* 6). ( $\times 487$ .)
- Fig. 24. Section (9-2-1) through the disc, peripherally to fig. 23, showing a vacuolated deep disc-cell (*dpc.*) and a yolk-laden cell (*dc.*), either a sub-disc cell or a deep disc-cell, not completely delimited. See text, p. 22. ( $\times 487$ .)

## LC 6 (K.15.8.30).

- Fig. 25. Section (5-3-3) passing just to one side of the centre of the disc which is here clearly delimited only over a small area to the left of its central region. In the preceding section it is delimited over its extent. Below the peripheral region the yolk-membrane (*ym.*) is distinct. ( $\times 250$ .)
- Fig. 26. Section (5-4-3) passing through the peripheral part of the central region of the disc, which is not sharply delimited below. *gp.*, gap through which yolk-spheres appear to gain access to the disc. *smv.*, sub-marginal vitellocyte. ( $\times 250$ .)



## PLATE V.

## LC 6 (K.15.8.30).

- Fig. 27. Section (3-3-3) through the disc, showing the central region and, on the right, the peripheral region. The central region overlying the central core of the yolk-bed is well delimited except over a small area (*gp.*) on the left. In the peripheral region two richly yolk-laden cells are still open to the yolk. ( $\times 170$ .)
- Fig. 28. Section (4-2-4) showing two peripheral vitellocytes (*pv.*), the larger on the left binucleate and in apparent continuity with the smaller on the right. See text, p. 26. ( $\times 346$ .)

## LC 7 (C.25.7.30).

- Fig. 29. Section (6-1-2) passing just to one side of the centre of the disc. The latter is sharply delimited from the yolk-bed, except over a small area (*gp.*) towards its right margin. *ybl.* yolk-ball. ( $\times 250$ .)
- Fig. 30. Section (8-2-2) to show the peripheral region of the disc. Yolk-membrane (*ym.*) distinct except in the region (*gp.*) towards the left. ( $\times 256$ .)

## B.15.7.30.

- Fig. 31. Section (7-2-2) through the peripheral region of the disc, showing the deep cells clearly delimited from the yolk-bed and the large yolk-laden cells (*yc.*) forming its periphery. *sdc.*, sub-disc cell. ( $\times 357$ .)
- Fig. 32. Section (9-2-2) showing the abnormal thickening at the periphery of the disc. See text, p. 28. ( $\times 340$ .)

## PLATE VI.

## VVH 36.

- Fig. 33. Surface view of blastodisc. See text, p. 34. ( $\times$  about 70.)
- Fig. 34. Section (4-3-5) of the disc, a little to one side of its centre. *pd.*, peripheral disc-cell. *ybl.*, yolk-ball. ( $\times 186$ .)
- Fig. 35. Section (6-2-5) just to one side of the centre of the disc, showing its marginal region. *pd.*, peripheral disc-cell. *pv.*, peripheral vitellocyte with a slight groove on its outer side. ( $\times 186$ .)

## VVH 17.

- Fig. 36. Surface view of blastodisc. ( $\times$  about 80.)
- Fig. 37. Section (7-5-4) through the disc, just to one side of its centre. ( $\times 175$ .)
- Fig. 38. Section (2-1-5) showing the margin of the disc and the adjoining marginal zone of the yolk. *pd.*, peripheral disc-cell. *pv.*, peripheral vitellocyte. ( $\times 856$ .)
- Fig. 39. Opposite margin to that of the preceding figure, showing the peripheral disc-cell (*pd.*), a peripheral vitellocyte (*pv.*) and a sub-marginal vitellocyte (*smv.*). ( $\times 700$ .)

## PLATE VII.

## VVH 17.

Fig. 40. Section (8-1-5) showing the peripheral disc-cell (*pd.*), a peripheral vitellocyte (*pv.*), a sub-marginal vitellocyte (*smv.*) and the cytoplasmic reticulum in the yolk (*cre.*). ( $\times 525$ .)

Fig. 41. Section (6-1-5) showing the marginal region of the disc. Note especially the connections of the peripheral disc-cell (*pd.*) with the adjoining peripheral vitellocyte (*pv.*) and the cytoplasmic reticulum (*cre.*) in the yolk. ( $\times 856$ .)

## VVH 37.

Fig. 42. Surface view of blastodisc. ( $\times$  about 80.)

Fig. 43. Section (9-1-5) through the disc. ( $\times 213$ .)

## VVH 41.

Fig. 44. View of entire egg with blastodisc. ( $\times$  about 14.)

Fig. 45. Surface view of blastodisc, more highly magnified. ( $\times$  about 60.)

## PLATE VIII.

## VVH 41.

Fig. 46. Section (10-4-5) through the disc. ( $\times 217$ .)

*Platypus* B & BB.

Fig. 47. Section (1-3-2) of the disc of B. ( $\times 300$ .)

Fig. 48. Section (3-3-2) through the egg, including the central region of the blastodisc, of BB. *yn.*, latebral neck. See text, p. 41. ( $\times 115$ .)

Fig. 49. Section (4-3-2) showing about half the disc of BB. ( $\times 324$ .)

## VVH 4.

Fig. 50. Surface view of blastodisc. ( $\times$  about 70.)

Fig. 51. Section (1-4-4) passing through the centre of the disc. ( $\times 220$ .)

## PLATE IX.

*Echidna* XVII.

Fig. 52. Section (4-4-3) through the blastodisc. ( $\times 200$ .)

Fig. 53. Portion of section (6-3-4), 0.07 mm. beyond the margin of the disc, showing a vitellocyte (*pv.*) in the prophase of division. *zp.*, zona, here very distinct. ( $\times 440$ .)

## VVH 30.

Fig. 54. Section (3-4-7) through the disc. ( $\times 247$ .)

## VVH 35.

Fig. 55. Surface view of blastodisc. ( $\times$  about 60.)

Fig. 56. Section (9-3-4) through the centre of the disc. *gr.*, germ-ring. *pv.* and *smv.*, peripheral and sub-marginal vitellocytes. ( $\times 210$ .)



- Fig. 57. Section (1-3-4) through the disc, the eighth to one side of the preceding. A large sub-marginal vitellocyte (*smv.*) lies below its central region and a smaller one nearer its left margin. ( $\times 300.$ )

## PLATE X.

## VVH 35.

- Fig. 58. Section (1-2-4) showing the marginal region of the disc, especially to illustrate a stage in the formation of the germ-ring. A binucleate sub-marginal vitellocyte (*smv.*) underlies the peripheral disc-cell, which is attached to its surface and is in continuity with a peripheral vitellocyte (*pv.*). ( $\times 965.$ )
- Fig. 59. Sections (8 and 9-3-4 combined), showing the marginal region of the disc. The peripheral disc-cell (*pd.*) is attached to a slight projection from the underlying peripheral vitellocyte (*pv.*), which is itself in continuity with a second peripheral vitellocyte. (See text, p. 47.) ( $\times 675.$ )
- Fig. 60. Section (1-3-4) of the opposite margin of the disc to that in the preceding figure, showing the peripheral disc-cell (*pd.*) and the completed germ-ring (*gr.*). ( $\times 450.$ )
- Fig. 61. Tangential section (9-2-5) showing the germ-ring and, on the left, three vitellocytes (*pv.* 1-3) not yet completely incorporated in it. ( $\times 380.$ )

## VVH 27.

- Fig. 62. Surface view of blastodisc. ( $\times$  about 50.)
- Fig. 63. See Pl. XI.

## VVH 14.

- Fig. 64. Surface view of blastodisc. ( $\times$  about 50.)

## PLATE XI.

## VVH 27.

- Fig. 63. Section (2-4-5) of disc, just to one side of its centre. *gr.*, germ-ring. ( $\times 210.$ )

## VVH 14.

- Fig. 64. See Pl. X.
- Fig. 65. Section (3-3-5) through centre of blastodisc. *gr.*, germ-ring. ( $\times 197.$ )
- Fig. 66. Section (9-2-5) showing the marginal region of the disc, the germ-ring (*gr.*) and a yolk-bed cell (*ybc.*), probably a sub-marginal vitellocyte. ( $\times 354.$ )

## VVH 9.

- Fig. 67. Surface view of blastodisc. ( $\times$  about 60.)
- Fig. 68. Section (3-2-5), a little to one side of the centre of the blastodisc and parallel to its long axis. ( $\times 190.$ )

## PLATE XII.

*Echidna* 30 (11.7.30).

- Fig. 69. View of the egg after removal of the shell, showing the oval blastoderm. ( $\times$  about 15.5.)
- Fig. 70. Section (5-1-3) showing portion of the blastoderm to one side of its centre, with a superficial and a deep primitive endoderm cell (*pr.end.*). *ybl.*, yolk-ball. ( $\times$ 1080.)
- Fig. 71. Section (5-2-3) showing portion of the blastoderm in the region of the central core of the yolk-bed, with at least two deep primitive endoderm cells (*pr.end.*). ( $\times$ 1080.)
- Fig. 72. Section (5-5-2) showing portion of blastoderm with a deep primitive endoderm cell (*pr.end.*) and a presumed endodermal mother-cell (*emc.*) ( $\times$ 1080.)
- Fig. 73. Section (4-4-2) through the marginal region of the blastoderm and the germ-ring (*gr.*). ( $\times$ 330.)
- Fig. 74. Section (1-3-3) showing the yolk-laden character of the cells of the marginal region of the blastoderm and the germ-ring (*gr.*), with a small papilliform projection overlapping the margin of the peripheral disc-cell (*pd.*). ( $\times$ 350.)

VVH 47.

Figs. 75 &amp; 76. See Pl. XIII.

- Fig. 77. Section (7-4-5) showing portion of the blastoderm just to one side of its centre. ( $\times$ 388.)

## PLATE XIII.

VVH 47.

- Fig. 75. View of the egg after removal of the shell, showing the blastoderm. See text, p. 57. ( $\times$  about 14.)
- Fig. 76. Section (9-4-5) through the centre of the blastoderm, and including its entire width. ( $\times$ 168.)
- Fig. 77. See Plate XII.
- Fig. 78. Section (4-4-5) showing a portion of the peripheral region of the blastoderm with a deep primitive endoderm cell (*pr.end.*). ( $\times$ 1000.)
- Fig. 79. Portion of central region of section (6-4-5) showing the blastoderm with two primitive endoderm cells (*pr.end.*). ( $\times$ 1066.)
- Fig. 80. Peripheral region of section (9-2-5) showing the blastoderm with two primitive endoderm cells (*pr.end.*) and a deep prospective ectoderm cell (*p.ect.*). ( $\times$ 1040.)
- Fig. 81. Portion of central region of section (4-3-6) showing a presumed endodermal mother-cell (*emc.*) in the blastoderm, here one-layered. ( $\times$ 1063.)
- Fig. 82. Corresponding region in section (2-2-5) showing a deep endodermal mother-cell (*emc.*). ( $\times$ 1100.)
- Fig. 83. Peripheral region of the blastoderm in section (4-4-5) showing the peripheral cell (*pd.*) attached to the surface of the germ-ring (*gr.*) by a short process. ( $\times$ 550.)



## PLATE XIV.

## VVH 47.

- Fig. 84. Periphery of blastoderm and germ-ring (*gr.*) in section (8-1-6), showing the peripheral cell (*pd.*) connected by a short process with a slight projection from the germ-ring and underlain by a large yolk-laden cell, as also is the cell adjacent to it. ( $\times 530$ .)
- Fig. 85. Peripheral region of the blastoderm and the germ-ring (*gr.*) in section (8-4-5). The peripheral cell (*pd.*) is closely adherent to the surface of the germ-ring, and directly below it is a large buried deep cell (*bdc.*). ( $\times 530$ .)

## VVH 45.

- Figs. 86 *a*, 86 *b* & 86 *c*. Section (8-1-5) a little to one side of the centre of the blastoderm, showing its entire width on one side from the central region in (*a*), to the germ-ring (*gr.*) in (*c*). *dgc.*, degenerate cell. *sp.*, sperms in zona-albumen layer. ( $\times 375$ .)
- Fig. 87. Section (5-2-5) close to the centre of the blastoderm and showing its central region. *ybn.*, yolk-bed nuclei. ( $\times 525$ .)

## PLATE XV.

## VVH 45.

- Fig. 88. Portion of central region of section (2-4-4), showing the blastoderm with two presumed endodermal mother-cells (*emc.*), one (on the left) reaching the surface, the other deep. *dgc.*, degenerating cell. *p.ect.*, periphery of yolk-laden prospective ectoderm cell. *ybl.*, yolk-ball. ( $\times 930$ .)
- Fig. 89. Central region of section (7-4-4) showing the blastoderm with two primitive endoderm cells (*pr.end.*), one on the right, in the metaphase, the other deep. ( $\times 980$ .)
- Fig. 90. Peripheral region of section (5-4-5) showing a prospective ectoderm cell (*p.ect.*) in process of insinuating itself into the single layered blastoderm. ( $\times 1200$ .)

## VVH 6.

- Fig. 91. View of egg after removal of the shell, showing the blastoderm in surface view. ( $\times$  about 14.)
- Figs. 92 *a*, 92 *b* & 92 *c*. Section (1-2-5) through the centre of the blastoderm showing its entire width on one side from the central region (*a*) to the germ-ring (*gr.*) in (*c*). ( $\times 440$ .)

## PLATE XVI.

## VVH 6.

- Fig. 93. Section (5-2-5) just to one side of the centre of the blastoderm. *dgc.*, degenerating cell. *pr.end.*<sup>1</sup>, primitive endoderm cell in the prophase. *ybn.*, yolk-bed nucleus. ( $\times 437$ .)
- Fig. 94. Central region of section (7-2-5) showing the blastoderm, with two primitive endoderm cells (*pr.end.*) intercalated at the surface. ( $\times 1000$ .)

Fig. 95. Central region of section (4-3-5) of the blastoderm, showing a primitive endoderm cell (*pr.end.*) with a conical process insinuating itself into the surface layer and a deep prospective ectoderm cell (*p.ect.*) in the anaphase. ( $\times 984$ .)

Fig. 96. A small area just outside the periphery of the central region in section (2-5-5), showing the blastoderm and a large irregular mass of nucleated cytoplasm (*ybn.*) in the yolk-bed (see text, p. 68). On the right, the blastoderm is formed by a group of cells (three superficial and one deep), probably primitive endoderm cells. ( $\times 632$ .)

VVH 32.

Fig. 97. See Plate XVII.

Fig. 98. Section (9-3-5) showing the unilaminar character of the blastodermic membrane. ( $\times 750$ .)

#### PLATE XVII.

VVH 32.

Fig. 97. View of the egg after removal of the shell, showing the blastoderm. ( $\times$  about 14.)

Fig. 98. See Pl. XVI.

Fig. 99. Section (2-4-5) showing a portion of the unilaminar blastodermic membrane, with an intercalated endodermal mother-cell (*emc.*). ( $\times 937$ .)

Fig. 100. Section (4-4-4) showing a portion of the blastodermic membrane with two intercalated primitive endoderm cells (*pr.end.*), probably sister-cells. ( $\times 960$ .)

Fig. 101. Section (7-5-4) showing an endodermal mother-cell (*emc.*) intercalated in the blastoderm. ( $\times 1143$ .)

Fig. 102. Section (8-1-5) showing a spheroidal primitive endoderm cell (*pr.end.*) intercalated in the blastoderm. ( $\times 905$ .)

Fig. 103. Section (3-2-5) showing a partially intercalated primitive endoderm cell (*pr.end.*) in the prophase. ( $\times 1100$ .)

VVH 42.

Fig. 104. Portion of the unilaminar blastoderm from the central region of section (1-4-5), here composed exclusively of prospective ectoderm cells. ( $\times 937$ .)

Fig. 105. Portion of the blastoderm from section (4-4-5), showing an intercalated primitive endoderm cell (*pr.end.*). *dgc.*, degenerate deep cell. ( $\times 750$ .)

#### PLATE XVIII.

VVH 42.

Fig. 106. Portion of the blastoderm from section (4-4-5) with an intercalated spheroidal primitive endoderm cell (*pr.end.*) ( $\times 950$ .)

Fig. 107. Portion of the blastoderm, section (1-3-6), showing a primitive endoderm cell (*pr.end.*), an endodermal mother-cell (*emc.*) and a prospective ectoderm cell (*p.ect.*). ( $\times 930$ .)



- Fig. 108. Portion of the blastoderm, section (3-2-3), showing two presumed endodermal mother-cells (*emc.*) and between the two, a prospective ectoderm cell and one on the right displaced. ( $\times 980$ .)
- Fig. 109. Portion of blastoderm, section (1-1-3), showing a primitive endoderm cell (*pr.end.*), a second (*pr.end.*<sup>1</sup>), apparently in the anaphase, and a fusiform prospective ectoderm cell. ( $\times 1150$ .)
- Fig. 110. Section (9-1-6) showing a large degenerate multinucleate cell. See text, p. 73. ( $\times 825$ .)
- Fig. 111. Section (1-1-6) showing the blastoderm and an exceptionally large yolk-bed nucleus (*ybn.*). See text, p. 73. ( $\times 950$ .)

## VVH 25.

- Fig. 112. Portion of the unilaminar blastoderm from section (8-5-3), here composed solely of prospective ectoderm cells. ( $\times 940$ .)
- Fig. 113. Portion of the blastoderm, section (8-5-4), showing an intercalated primitive endoderm cell (*pr.end.*) ( $\times 730$ .)
- Fig. 114. Tangential section (1-1-1). Portion of the blastoderm viewed on the flat, showing the flattened polygonal form of the large prospective ectoderm cells and, at the right lower corner, two *pr.end.* sister-cells, the nucleus in one not yet reconstituted. ( $\times 910$ .)

## PLATE XIX.

*Echidna* IV.

- Fig. 115. Section (4-2-4) through the central region of the blastoderm and the underlying yolk-bed, the central core of which is greatly vacuolated. The blastoderm is composed of spindle-shaped prospective ectoderm cells, with two primitive endoderm cells (*pr.end.*) in process of becoming deep. ( $\times 340$ .)
- Fig. 116. Portion of blastoderm, section (8-1-4), showing five *pr. end.* cells, two of them deep (*pr.end.d.*), two still intercalated but slightly overlapped by the margins of the adjoining *pros. ect.* cells and the fifth (*pr.end.*<sup>1</sup>) intercalated, but provided with a process (*pr.*) which underlies the *pros. ect.* cell on the right of the figure. ( $\times 1125$ .)
- Fig. 117. Portion of blastoderm, section (6-3-4), with three intercalated *pr. end.* cells (*pr.end.*) in contact and an isolated deep cell (*pr.end.d.*). ( $\times 763$ .)
- Fig. 118. Portion of blastoderm, section (3-3-3), showing three intercalated *pr. end.* cells (*pr.end.*), the one on the right partially underlying the adjoining *pros. ect.* cell. ( $\times 763$ .)
- Fig. 119. Portion of blastoderm, section (3-4-2), showing a *pr. end.* cell (*pr.end.*), the major portion of whose body has slipped under the adjoining *pros. ect.* cell and which is provided with a slender process on the left, overlapping the thin margin of a *pros. ect.* cell. ( $\times 857$ .)
- Fig. 120. Section (2-5-2) showing a *pr. end.* cell (*pr.end.*) still in contact with the zona-albumen layer, but with a thick process (*pr.*) underlying the adjacent *pros. ect.* cell. ( $\times 1300$ .)

- Fig. 121. Section (1-2-4) showing a deep pr. end. cell (*pr.end.d.*), possessing a long finely granular process (*pr.*). ( $\times 1300$ .)
- Fig. 122. Section (3-2-3), showing two intercalated pr. end. cells (*pr.end.*), one in the metaphase, the other provided with a short conical process underlying the margin of a pros. ect. cell. ( $\times 857$ .)
- Fig. 123. Portion of the blastoderm, section (4-3-4), showing an obliquely disposed intercalated pr. end. cell (*pr.end.*) in the anaphase. ( $\times 860$ .)
- Fig. 124. Tangential section (1-3-7). A small portion of the blastoderm, seen on the flat from the inner surface, showing two pros. ect. cells (*p.ect.*) and three pr. end. cells, one of them certainly deep (*pr.end.d.*) and provided with a tapering process (*pr.*). ( $\times 980$ .)

## PLATE XX.

*Echidna* IV.

- Fig. 125. Section (2-3-2) of the blastoderm, showing two large degenerate cells, one intercalated, the other deep. ( $\times 750$ .)
- Fig. 126. Section (1-5-4) showing the germ-ring (*gr.*) and the peripheral disc-cell (*pd.c.*) attached to it. ( $\times 740$ .)

*Echidna* XVIII.

- Fig. 127. Tangential section (2-1-1). A small fragment of the blastoderm, seen on the flat from the inner surface, showing three deep pr. end. cells connected by their processes and the nuclei of two pros. ect. cells (*p.ect.*). ( $\times 1200$ .)
- Fig. 128. Tangential section (6-1-1) showing a curiously elongated pr. end. cell, with two processes, one long and curved. See text, p. 80. ( $\times 1200$ .)
- Fig. 129. Tangential section (4-2-1) showing a pr. end. cell, irregularly triangular in outline, with two processes, one of them spatulate. ( $\times 1200$ .)

## VVH 8.

- Fig. 130. Section (4-4-6) showing the central region of the blastoderm, with five deep pr. end. cells and the much vacuolated superficial zone of the yolk-bed. ( $\times 608$ .)
- Fig. 131. See Pl. XXI.
- Fig. 132. Tangential section (3-1-1). A small portion of the blastoderm, viewed on the flat from the inner surface, showing two deep pr. end. cells and two pr. end. sister-cells (*sc.*) in the telophase, together with a pros. ect. cell (above) and a yolk ball (*ybl.*) below. ( $\times 750$ .)

## PLATE XXI.

## VVH 8.

- Fig. 131. Section (1-2-5) showing a portion of the blastoderm, with two pr. end. cells (*pr.end.*) in process of becoming deep and two pr. end. sister-cells (*sc.*) in the telophase and still intercalated. ( $\times 730$ .)



Fig. 133. Tangential section (3-1-1). Portion of the blastoderm, viewed on the flat from the inner surface, showing a group of six pr. end. cells (1-6) and three pros. ect. cells. See text, p. 82. ( $\times 1100$ .)

## VVH 3.

Fig. 134. Tangential section (2-1-1). Portion of the blastoderm, viewed on the flat from the outer surface, showing four pr. end. cells, (1-4), of which 1-3 are connected by their processes, and three pros. ect. cells. See text, p. 83. ( $\times 1125$ .)

## VVH 28.

Fig. 135. Section (1-4-6) through the central region of the blastoderm, showing the thin blastodermic membrane, here composed of pros. ect. cells and three deep pr. end. cells, two of them connected together and one of the two (*pr.end.*) provided with a tapering process. ( $\times 300$ .)

Fig. 136. Section (1-2-6) through the blastoderm, showing two pros. ect. cells (*p.ect.*) and six pr. end. cells, of which one is intercalated and provided with a short process (*pr.*), three are deep and two are sister-cells (*sc.*), one of them still intercalated. *dgc.*, degenerate cell. ( $\times 975$ .)

Figs. 137 & 138. See Pl. XXII.

Fig. 139. Section (8-3-3) showing two intercalated pr. end. cells and one, partially intercalated, obliquely placed and in the telophase of division. ( $\times 1125$ .)

Fig. 140. Section (6-4-4) showing a large intercalated pr. end. cell, with an elongated tapering process (*pr.*) underlying the adjacent pros. ect. cell; on its right a rounded cell in division, probably degenerating. ( $\times 1125$ .)

Fig. 141. Tangential section (1-4-8) showing a pros. ect. cell in the metaphase, the mitotic figure being situated in a clear "Mixoplasmic" area. See text, p. 85. ( $\times 1500$ .)

## PLATE XXII.

## VVH 28.

Fig. 137. Section (3-1-5) showing portion of the blastoderm, with two pros. ect. cells, three deep pr. end. cells and a fourth, on the left, possibly an endodermal mother-cell. *dgc.*, degenerate cell. ( $\times 1125$ .)

Fig. 138. Section (9-6-3) showing a portion of the blastoderm with two pr. end. sister-cells (*sc.*) in the late telophase, a partially intercalated pr. end. cell (*pr.end.*) with a conical process and a small pr. end. daughter-cell in the telophase. ( $\times 1000$ .)

Fig. 142. Tangential section (9-4-8). A small portion of the blastoderm, viewed on the flat from the inner surface, showing two elongated pr. end. cells of the bipolar type, and on the right three vacuolated pr. end. cells, one of them with a tapering process. Four pros. ect. cells are also visible. ( $\times 750$ .)

Fig. 143. Tangential section (9-4-8), inner surface view of a portion of the blastoderm, showing a sheet of five pros. ect. cells with light staining nuclei, and overlying them a group of six pr. end. cells (1-6) with vacuolated cytoplasm. Cell (1) is devoid of processes and slightly overlaps (2) and (5). Cell (2) gives off a short process on the right which joins cell (3) and a similar process from its lower angle which appears to connect with cell (5). Cell (3) is connected with cell (6) by a narrow anastomotic band overlying a pros. ect. nucleus, and gives off a longer (left) and a shorter (right) process. Cell (4), irregularly quadrangular, is produced above into a truncated projection, evidently the base of a broken-off process, and gives off three other processes, a broad tapering process on the left which overlaps cell (3), a slender process from its lower right margin and a thicker process from its lower angle, which widens out before reaching the level of the light-stained pros. ect. nucleus seen below it in the figure. ( $\times 1132$ .)

Fig. 144. Tangential section (9-4-8), as in preceding figure, showing four pros. ect. nuclei and five pr. end. cells (1-5). Cell (1), with cytoplasm much vacuolated, is produced towards the right, into a well-marked tapering process. Cell (2) is joined to (1) by a short process. Cell (4) is produced into a light staining, broad, bluntly ending expansion, and above that into a much smaller process terminating in a fine filament, overlying cell (2), whilst above and to the right, it gives off a spike-like process adjoining the pros. ect. nucleus. Cell (5), somewhat pear-shaped and with much vacuolated cytoplasm, gives off from its narrow end a slender process, terminating in a slight expansion. It fails to connect with the spike-like process of cell (4). ( $\times 1000$ .)

Fig. 145. Tangential section (8-4-8), as in the preceding figures, showing three pros. ect. cells and two pr. end. cells, connected by the junction of a short process from each, but fusion of the two is not yet complete. The larger cell gives off two other processes, a thicker one above and a more slender one from its left margin. The smaller cell shows a broken edge at its upper end, possibly indicative of a broken-off process, whilst its lower end is produced into two light staining expansions. ( $\times 1125$ .)

#### VVH 11.

Fig. 146. Section (3-3-5) through the blastoderm and yolk-bed, a little to one side of the centre, showing the continuous blastodermic membrane, with three underlying pr. end. cells, one of them fusiform (*pr.end.*). ( $\times 300$ .)

### PLATE XXIII.

#### VVH 11.

Fig. 147. Tangential section (3-1-1), portion of the blastoderm viewed on the flat from the outer surface, showing two pros. ect. cells and four pr. end. cells, of which the two uppermost are connected by a short anastomotic strand. ( $\times 1250$ .)



- Fig. 148. Tangential section (6-1-1), as in the preceding figure, showing three pros. ect. cells and six pr. end. cells. Three of the latter cells on the right are so connected by anastomoses as to form the beginning of an endodermal network. ( $\times 938$ .)
- Fig. 149. Tangential section (7-3-11), as in the preceding figure, but viewed from the inner surface, showing a pros. ect. cell and two pr. end. cells, the latter connected by a long anastomosis formed by a thick process from the cell on the left and a very thin process from the cell on the right. ( $\times 834$ .)
- Fig. 150. Tangential section (3-3-11), as in the preceding figure, showing two pros. ect. cells and six pr. end. cells of which four on the left are connected by anastomoses. ( $\times 938$ .)
- Fig. 151. Section (6-3-7) through the uncovered lower polar area of the egg (*lpa.*), with the germ-ring (*gr.*) on either side. ( $\times 170$ .)
- Fig. 152. High power view of the germ-ring (*gr.*) on the right side of the preceding figure. Note the attachment of the peripheral cell of the blastoderm (*bl.*) to its surface, immediately above the nucleus. ( $\times 680$ .)

## PLATE XXIV.

*Echidna* I.

- Fig. 153. Section (2-1-3) through the blastoderm and yolk-bed, a little to one side of the centre of the latter. The superficial layer of the blastoderm is purely ectodermal, and below it are situated six fusiform endoderm cells, apparently isolated. The central core of the yolk-bed is richly vacuolated. ( $\times 408$ .)
- Fig. 154. Section (8-3-3) through the peripheral region of the blastoderm. Below its superficial ectodermal layer, the definitive endoderm is becoming differentiated, and two yolk-spheres are in process of enclosure. ( $\times 402$ .)
- Fig. 155. Section (4-5-4) through the peripheral region of the blastoderm, showing a yolk-sphere in process of enclosure by two endodermal cells. ( $\times 500$ .)
- Fig. 156. Section (4-1-4) as in the preceding figure, showing three pr. end. cells (*pr.end.*) intercalated in the superficial layer and a fusiform endoderm cell (*end.*) below the latter. ( $\times 900$ .)
- Fig. 157. Section (11-4-4), as in fig. 155, showing a pr. end. cell (*pr.end.*) in the prophase intercalated in the superficial layer, the definitive endoderm (*end.*), and on the right a yolk-sphere enclosed in an endoderm cell (*end.*). ( $\times 745$ .)
- Fig. 158. Section (8-2-2), showing a pr. end. cell in the metaphase, the plane of division being slightly oblique to the surface, and illustrating also delayed completion of the splitting of certain of the chromosomes. ( $\times 1700$ .)
- Figs. 159-161. Sections (9, 7, and 4-2-6) illustrate the method of enclosure of a yolk-sphere by an endoderm cell and the occurrence of division in the latter during the process. See text, p. 91. ( $\times 1200$ .)

## PLATE XXV.

*Platypus S.*

- Fig. 162. Section (5-4-1) through the blastoderm and yolk-bed just to one side of the centre. The superficial layer composed of ectodermal cells is underlain by five endodermal cells, two of them connected. A granular coagulum is present between the blastoderm and the surface of the yolk-bed. ( $\times 413$ .)
- Fig. 163. Section (3-3-1) through the peripheral region of the blastoderm, showing the superficial ectodermal layer, and underlying it three pr. end. cells (*pr.end.*) and two fusiform endoderm cells (*end.*) connected together. ( $\times 750$ .)
- Fig. 164. Section (5-1-1), as in the preceding figure, showing the superficial ectodermal layer and below it on the left four endodermal cells (*end.*), three of them connected together. ( $\times 750$ .)

*Platypus SS.*

- Fig. 165. Section (9-1) through the blastoderm and the peripheral part of the central core of the yolk-bed. The blastoderm is now bilaminar and below it is the well-marked sub-germinal cavity (*sgc.*) containing traces of coagulum and on its floor a group of cells and free yolk-spheres. ( $\times 617$ .)
- Fig. 166. Section (1-1) showing the bilaminar blastoderm, the sub-germinal cavity (*sgc.*) with traces of coagulum and the peripheral region of the yolk-bed. ( $\times 617$ .)

*Echidna XIII.*

- Figs. 167 & 168. Sections (8-4-5 and 1-4-5) through the central and peripheral regions respectively of the yolk-navel. For description, see text, p. 94. *ect.m.*, ectodermal thickening. *gr.c.*, germ-ring cytoplasm. *gr.n.*, germ-ring nucleus. *nc.*, navel cavity. ( $\times 230$ .)

*Echidna XIV.*

- Fig. 169. Section (7-3-6) through the centre of the yolk-navel. See text, p. 95. *nc.l.*, lumen of the tubular prolongation of the ectodermal thickening (*ect.m.*) leading into the navel-cavity (*nc.*). ( $\times 230$ .)

## PLATE XXVI.

*Echidna IX.*

- Fig. 170. Section (5-4-3) a little to one side of the centre of the blastoderm, showing the superficial layer and three deep pr. end. cells and two intercalated cells, one of them in the metaphase (*pr.end.*, towards the left). ( $\times 250$ .)
- Fig. 171. Section (10-4-3) through the peripheral region of the blastoderm (*mbl.*) and the germ-ring (*gr.*), to show especially a group of some nine cells (*cgp.*) overlying the attachment of the fusiform peripheral cell of the blastoderm to the germ-ring and the presence of two sub-marginal cells (*smc.*). ( $\times 438$ .)



Fig. 172. Section (6-3-4), as in the preceding figure, showing again the cell-group (*cgp.*) overlying the attachment of the peripheral cell (*pc.*) to the germ-ring, but here it consists of only four cells, two of them large and laden with medium-sized yolk-spheres, whilst the peripheral cell (*pc.*) and the one next to it are large and oval in outline, not fusiform, as are those in the preceding figure. Only one sub-marginal cell (*smc.*) is present. ( $\times 438$ .)

*Echidna* TLB 1.

Fig. 173. Section (7-4-1) through the blastoderm and the yolk-bed, showing the superficial layer and three underlying pr. end. cells (*pr.end.*). ( $\times 750$ .)

Fig. 174. Section (6-2-2) showing the elongated loose mass of cyst-like bodies (*cys.*) and "spores" (*sp.*) of an undetermined parasitic organism situated in a split in the zona-albumen layer. *cys.*<sup>1</sup>, thin-walled cyst containing a granular material. *za.*, zona-albumen layer of practically normal thickness with a single layer of "spores" along its middle. See text, p. 100. ( $\times 195$ .)

*Echidna* XII.

Fig. 175. Composite figure from sections (6-3-5 and 5-2-5 (shell)) to show the structure of the secondary egg-envelopes. *za.*, the very thin zona, together with the dense albumen layer (0.009-0.010 mm. in thickness). *la.*, laminae of the outer more fluid layer of albumen (0.006-0.009 mm. in thickness). *sh.*, shell (0.012 mm. in thickness). *cgm.*, coagulum in space between the more fluid layer and the shell, a similar coagulum occurs between the laminae (*la.*). The width of the space below the shell, shown in the figure, has no observational basis, the shell in the sections having become widely separated from the laminated layer; in the intact egg it is probably quite narrow. ( $\times 900$ .)

PLATE XXVII.

*Sparrow.*

Fig. 176. Section (9-4-2) through the blastodisc of Sp. 13.3.6.19 (2.10 mm. in diameter  $\times$  0.08 mm. in thickness), showing the two types of cell composing it, viz. prospective endodermal cells, mostly large and crowded with small deeply staining yolk-spheres, and prospective ectodermal cells, smaller and with much finer, pale-staining yolk-granules. Between the blastodisc and the surface of the yolk-bed is the sub-germinal cavity. ( $\times 563$ .)

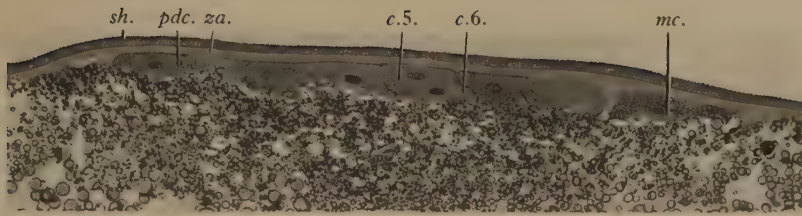
Fig. 177. Section (10-2-2) through the blastodisc of Sp. 2.6.16 A (about 2.09 mm. in diameter  $\times$  0.08 mm. in thickness), to show the migration inwards of yolk-rich prospective endodermal cells from amongst the light staining prospective ectodermal cells, now in process of forming an epithelial layer at the surface, the future ectoderm. ( $\times 563$ .)

Fig. 178. Section (8-2-2) through the blastodisc of Sp. 6.17 CC. (about 2.3 mm. in diameter  $\times$  0.072 mm. in thickness), showing the superficial layer (the future ectoderm) in process of differentiation in segments, discontinuous like the underlying spaces which separate them from the lower layer composed of prospective endodermal cells. Between these spaces are pillar-like areas of the blastodisc, formed largely of prospective endodermal cells in process of migrating inwards. Over the middle thick pillar in the figure is a surface-groove, indicative of active migration on the part of these cells, and two other less marked grooves are visible to the right of it. ( $\times$ 468.)

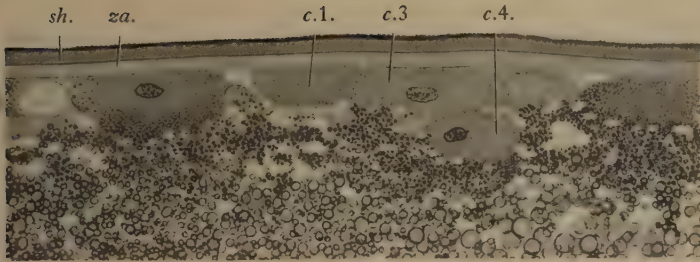
Fig. 179. Section (9-6-2) showing the marginal region and the adjoining portion of the marginal cytoplasmic zone in the blastodisc of Sp. 2.22.5.19 (about 2.29 mm. in diameter  $\times$  0.08 mm. in thickness). For description, see text, pp. 108-109. ( $\times$ 468.)



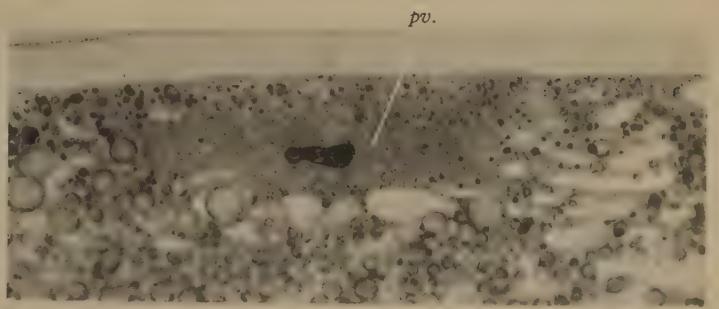




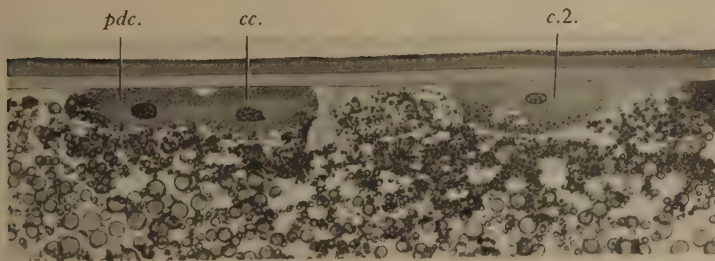
I



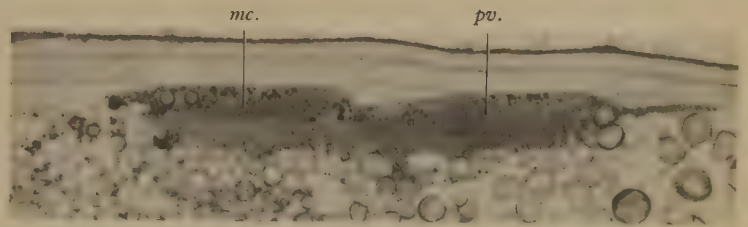
2



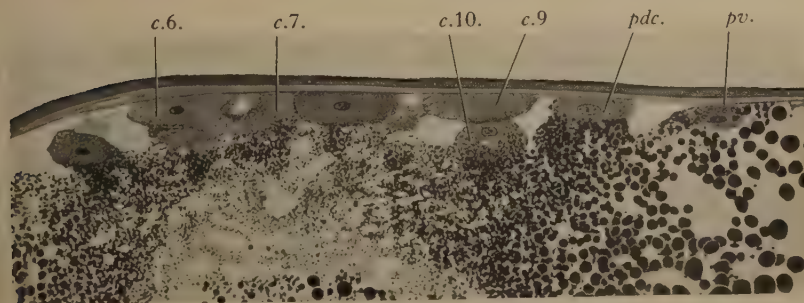
4



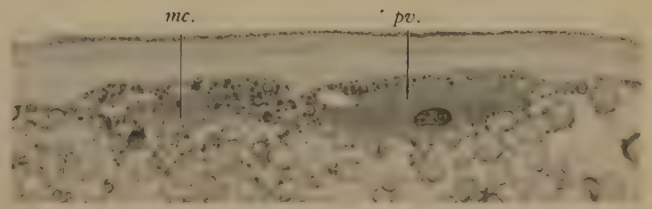
3



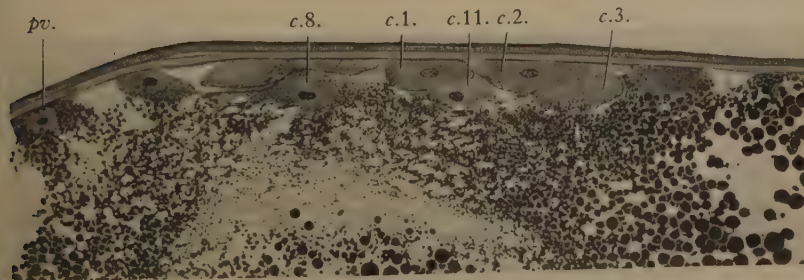
5a



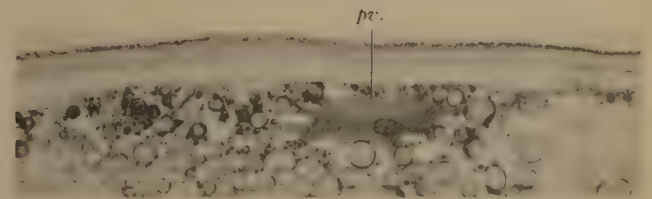
6



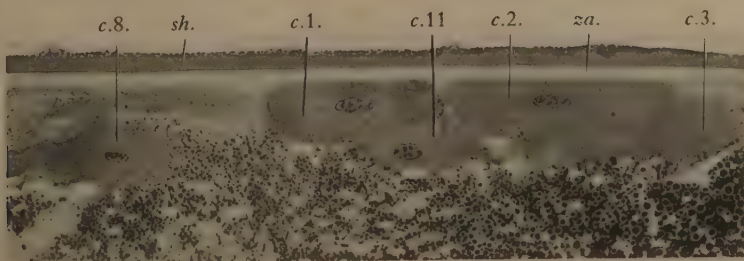
5b



7



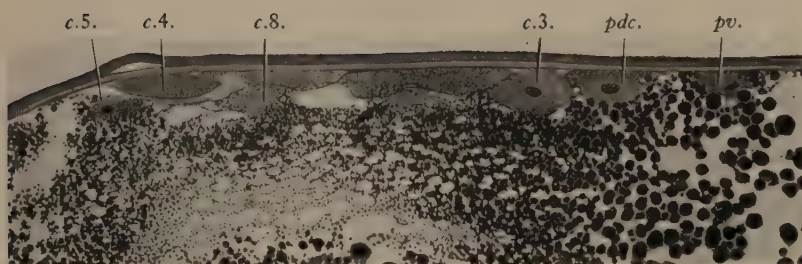
5c



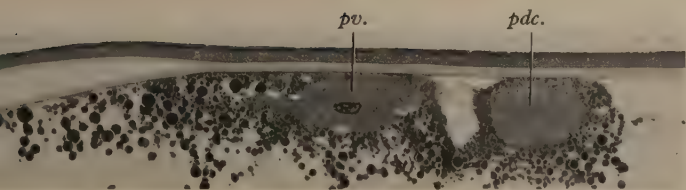
8



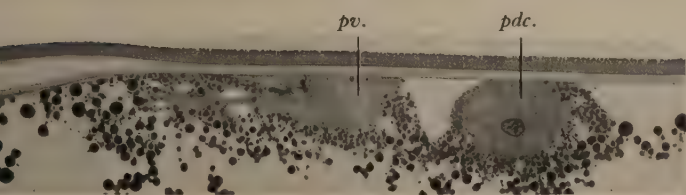




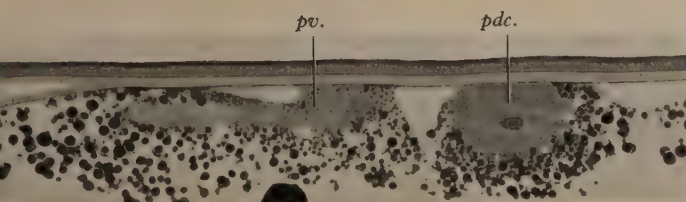
9



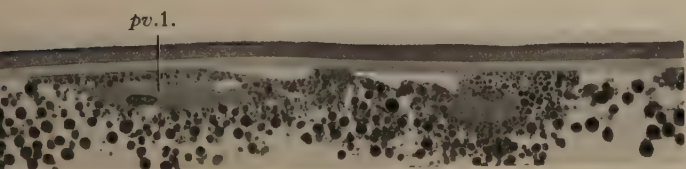
12a



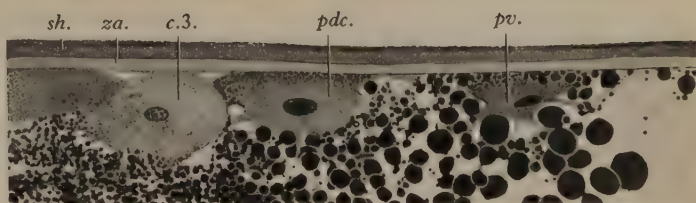
12b



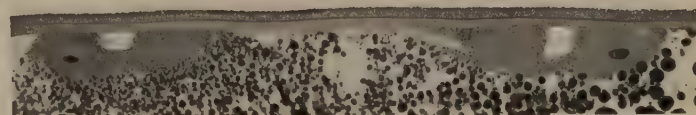
12c



12d



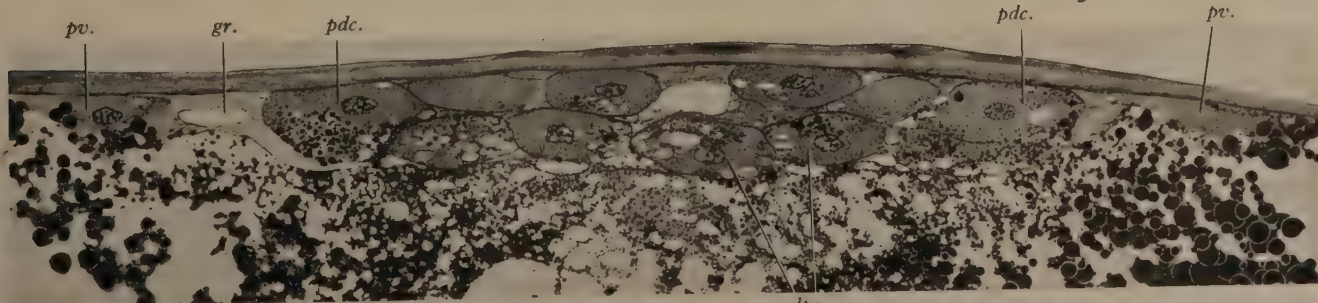
10



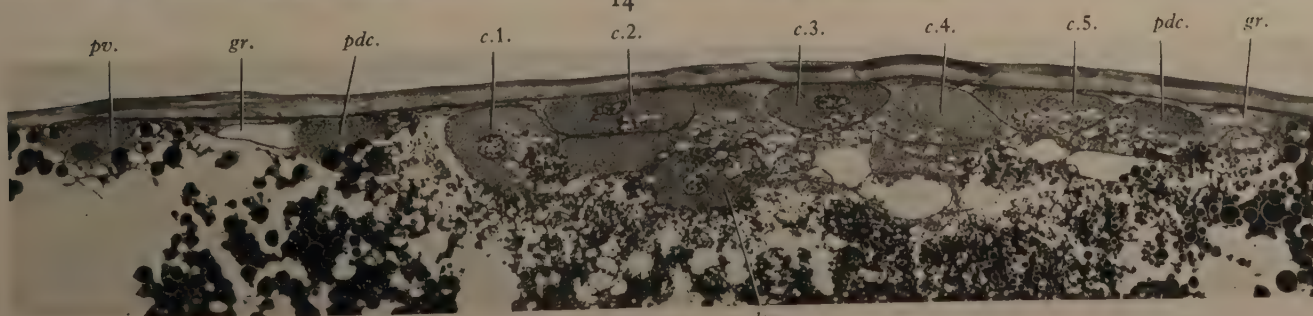
11



13



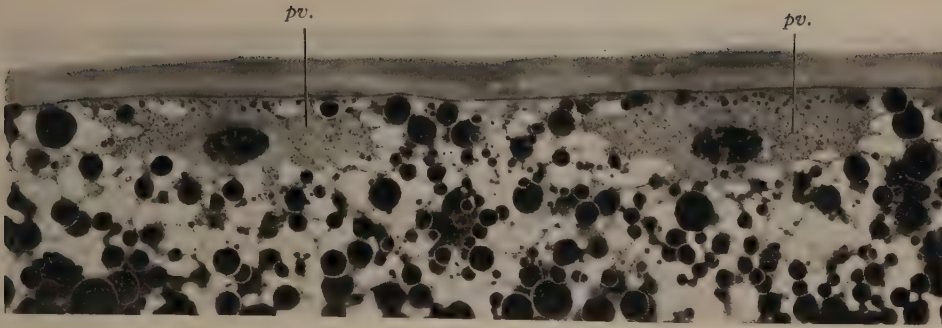
14



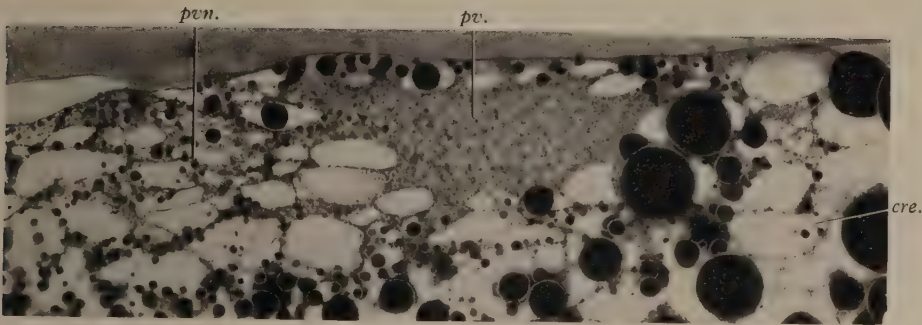
15



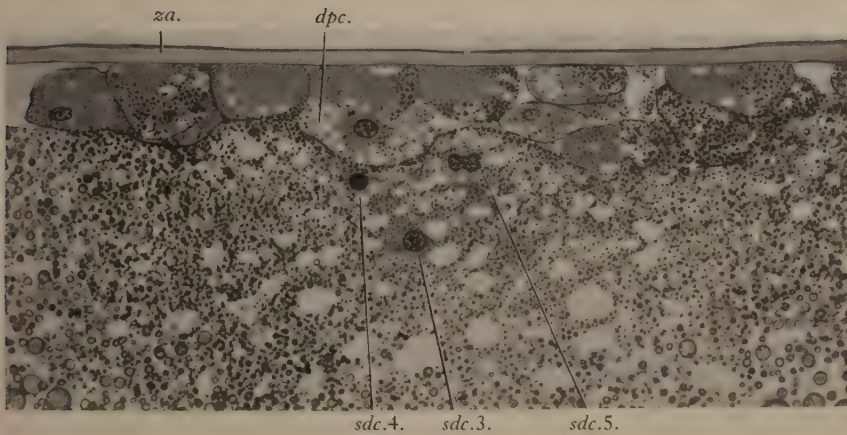




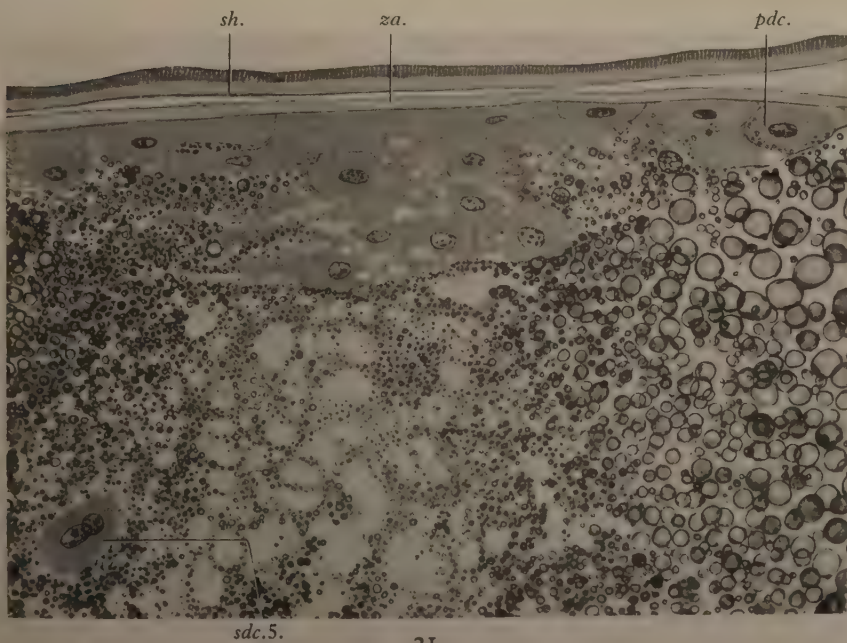
16



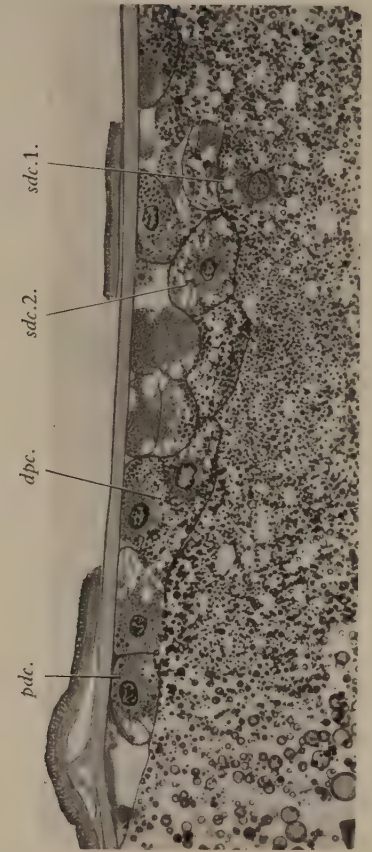
17



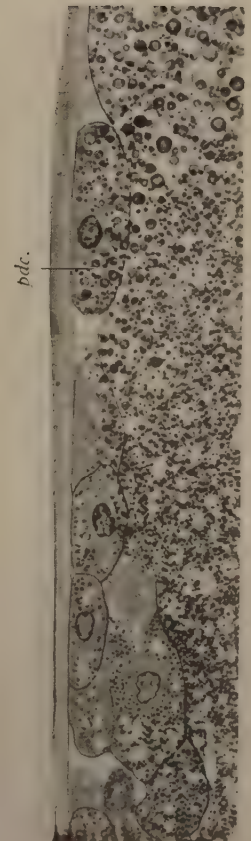
18



21



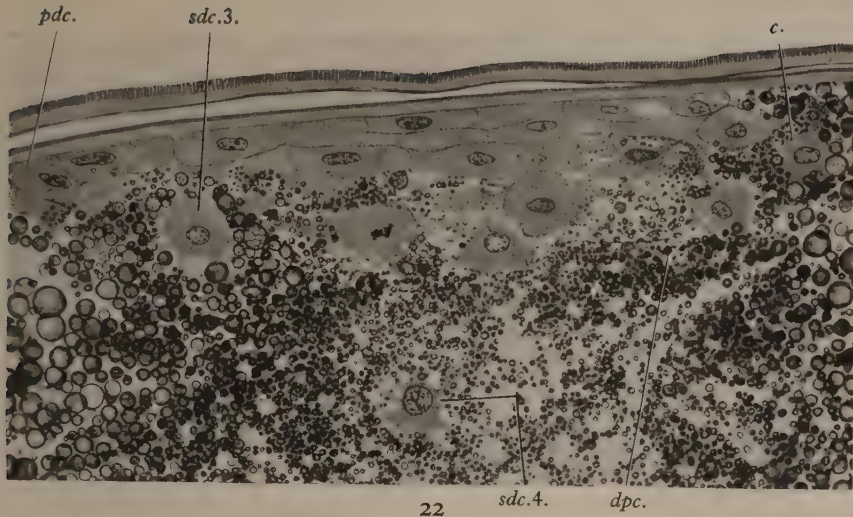
19



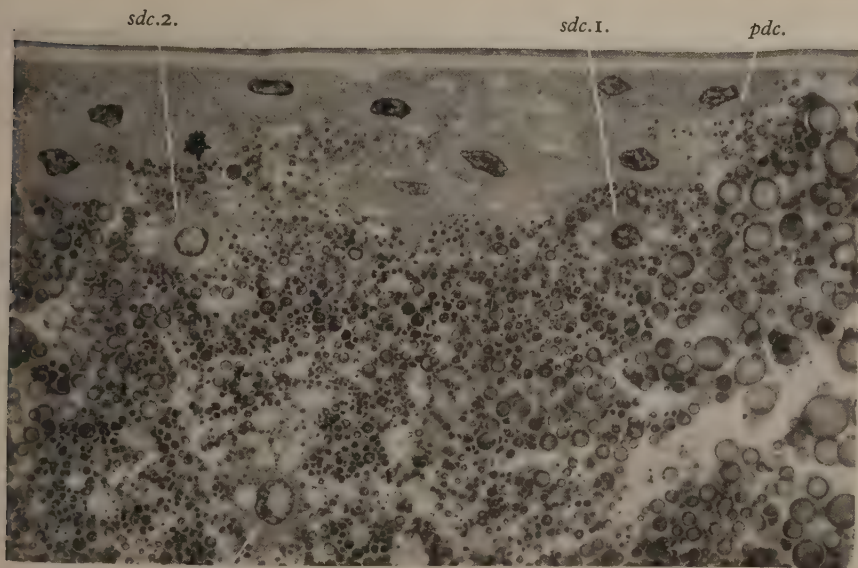
20



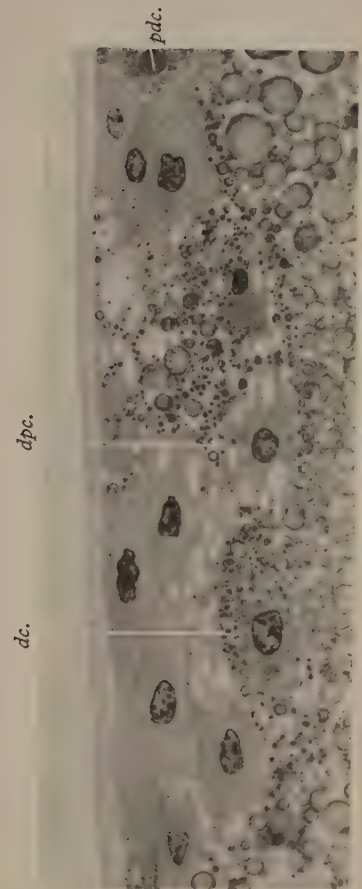




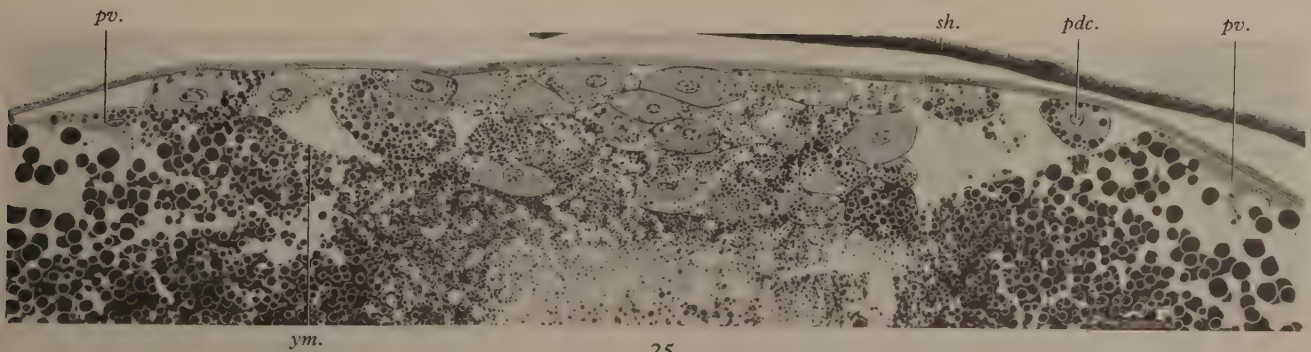
22



23



24



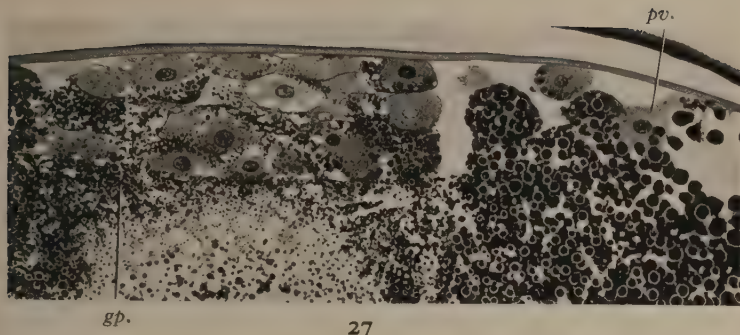
25



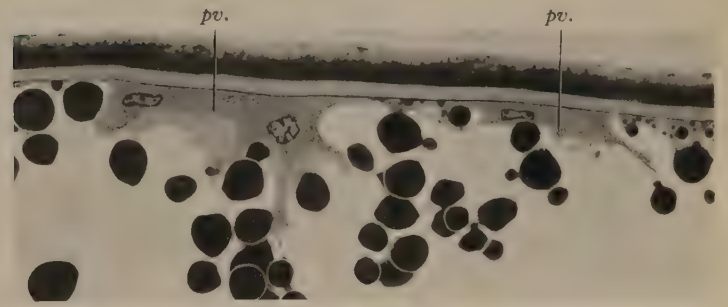
26







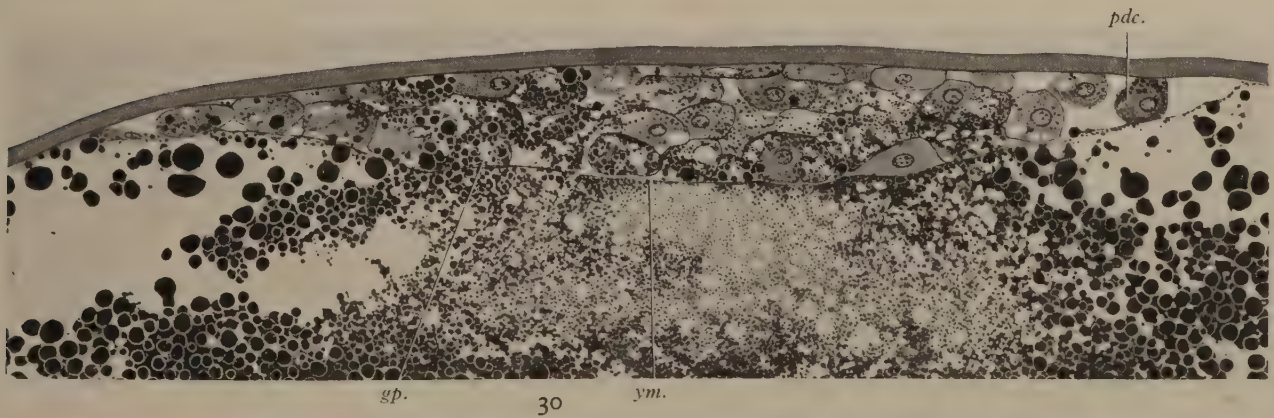
27



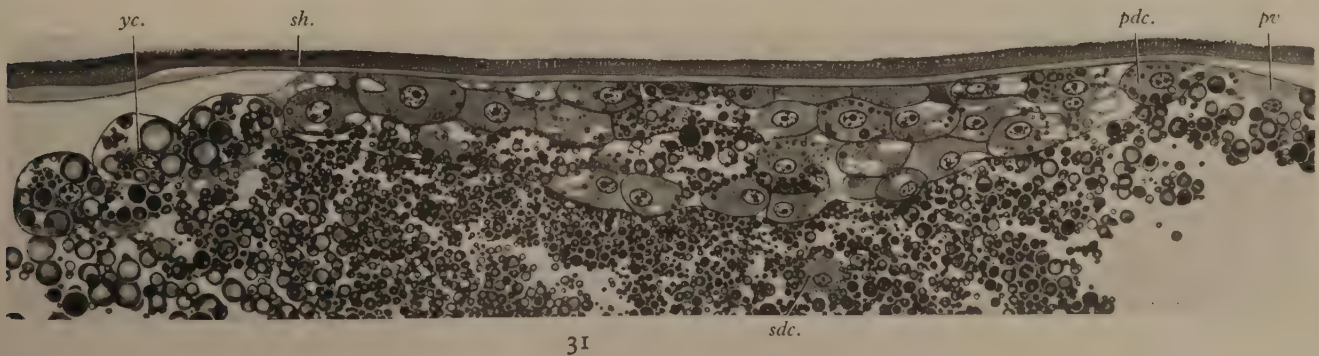
28



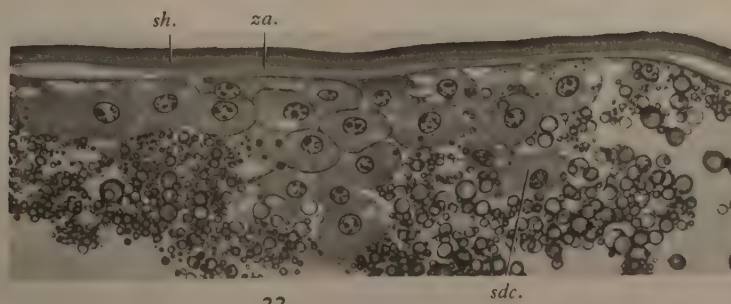
29



30



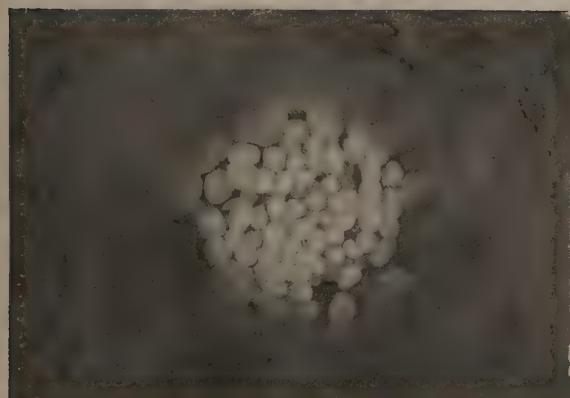
31



32



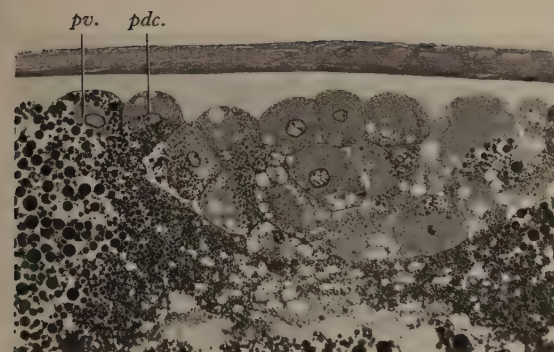
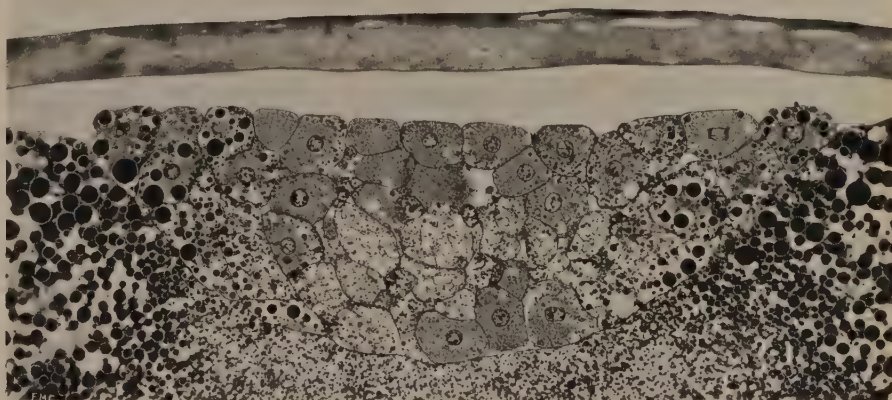




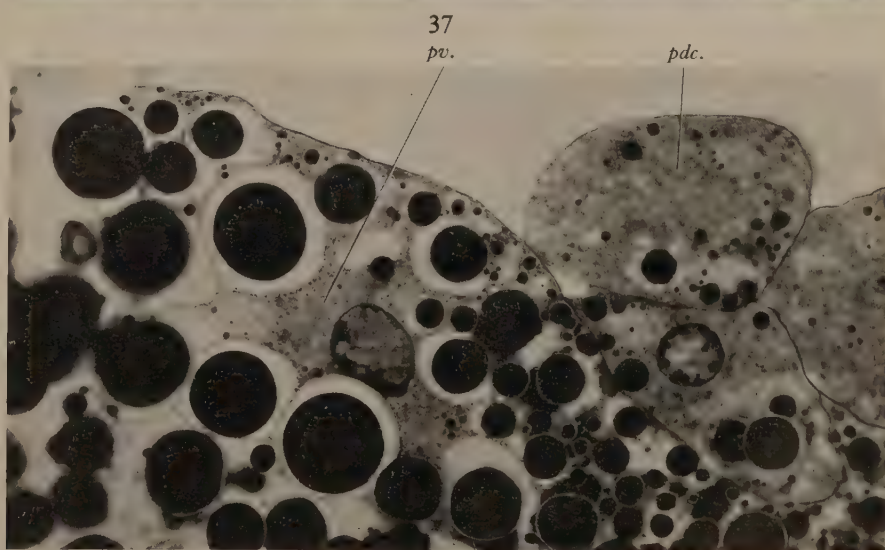
33



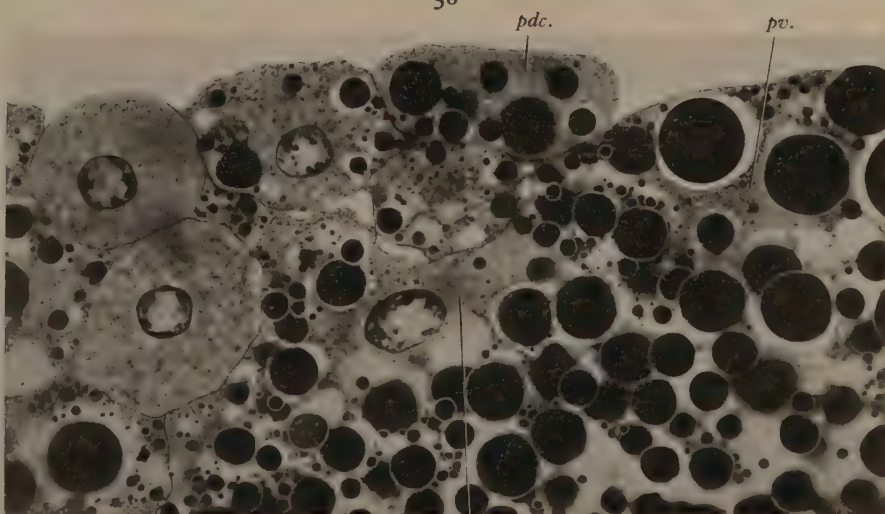
34



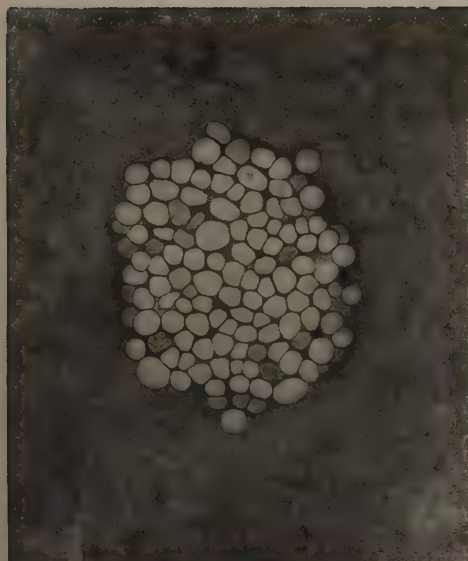
35



38



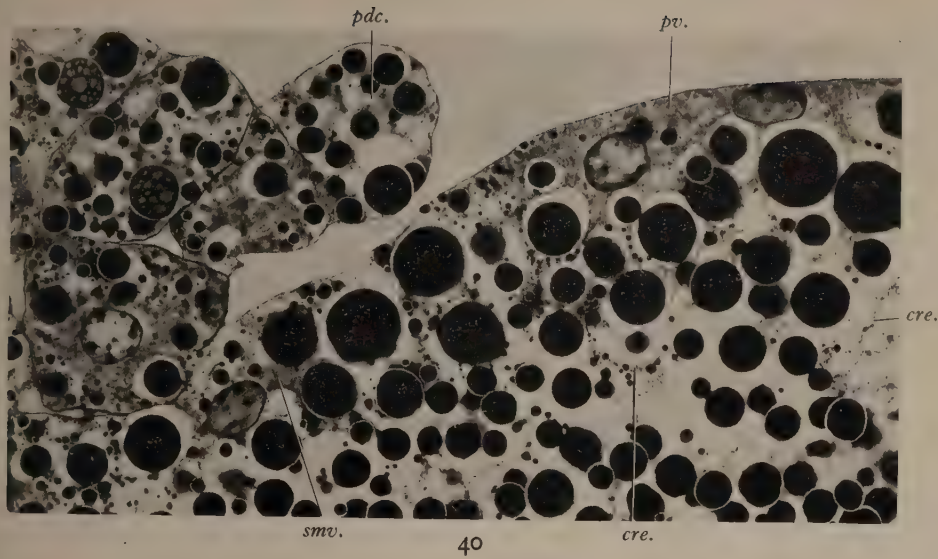
39



36



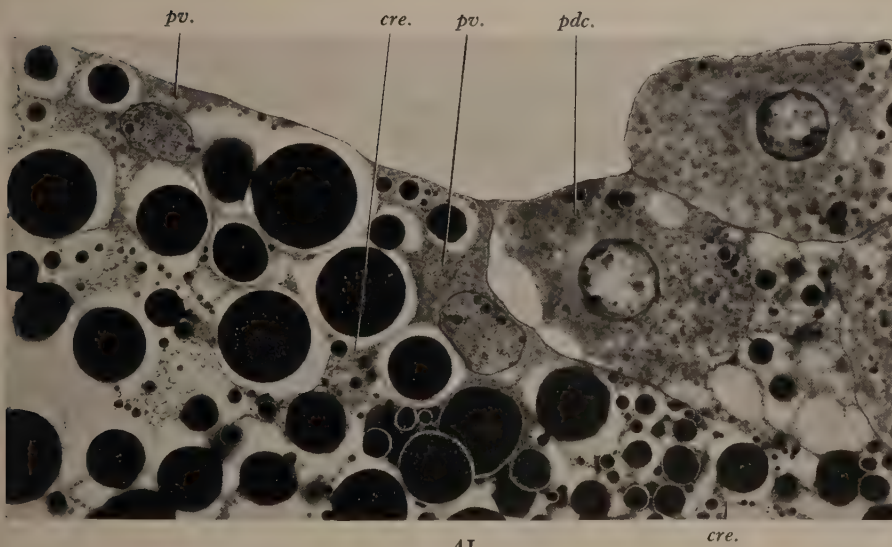




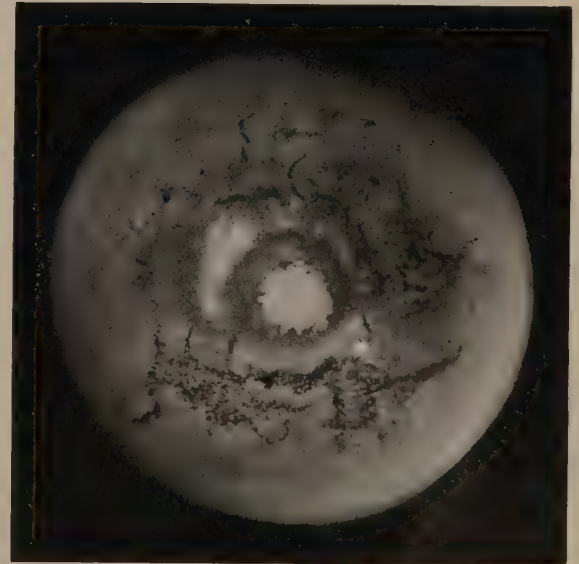
40



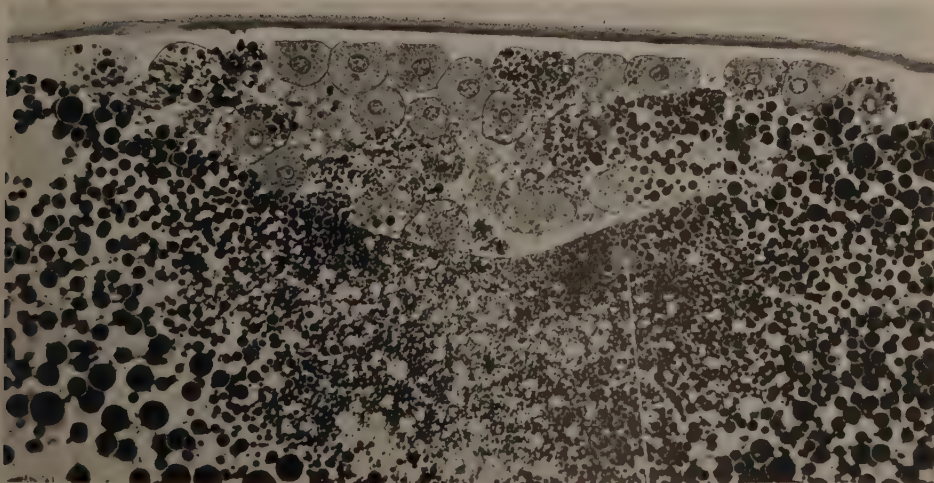
42



41



44



43



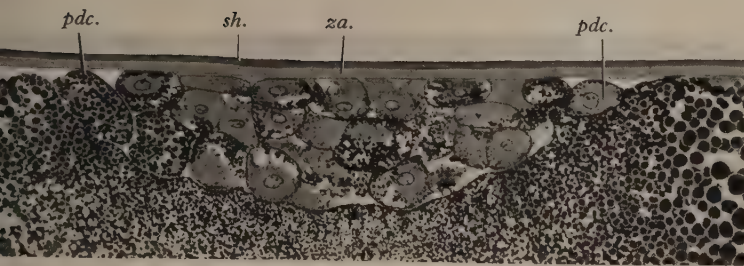
45



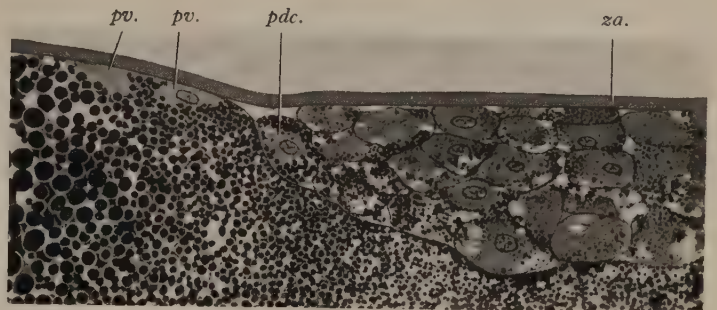




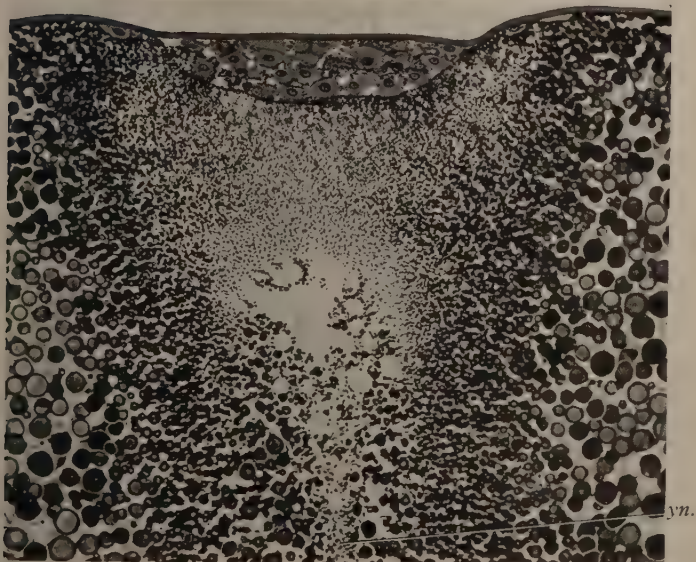
46



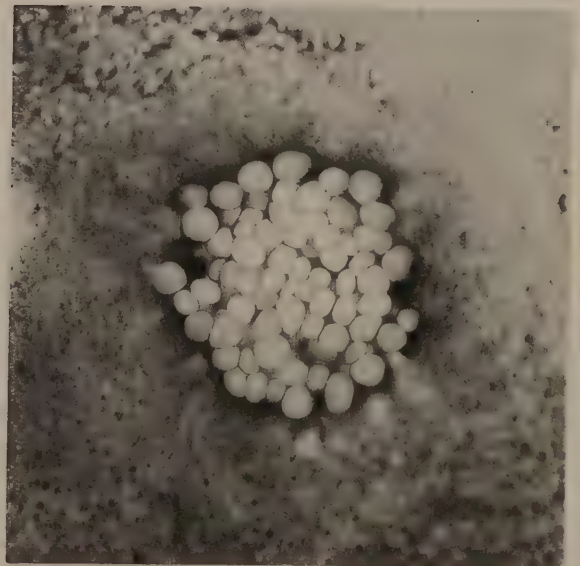
47



49



48



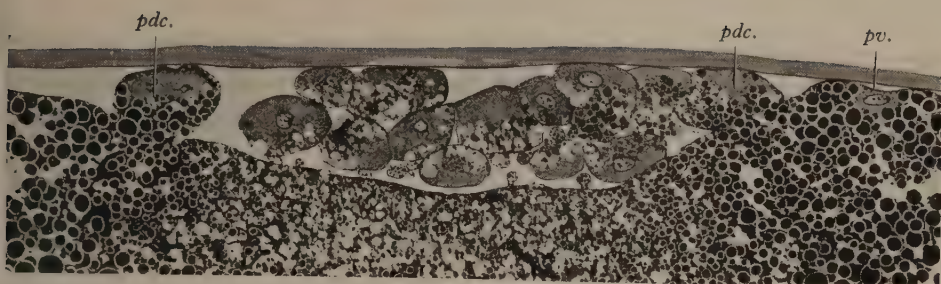
50



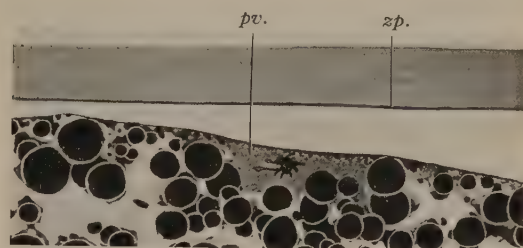
51



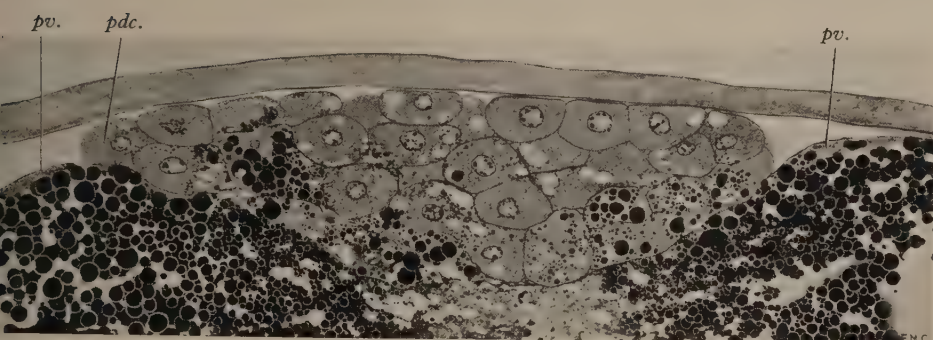




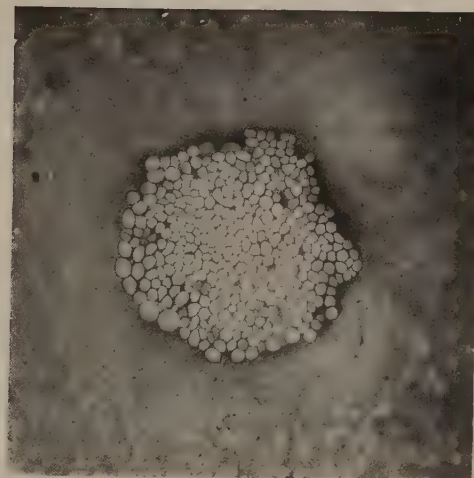
52



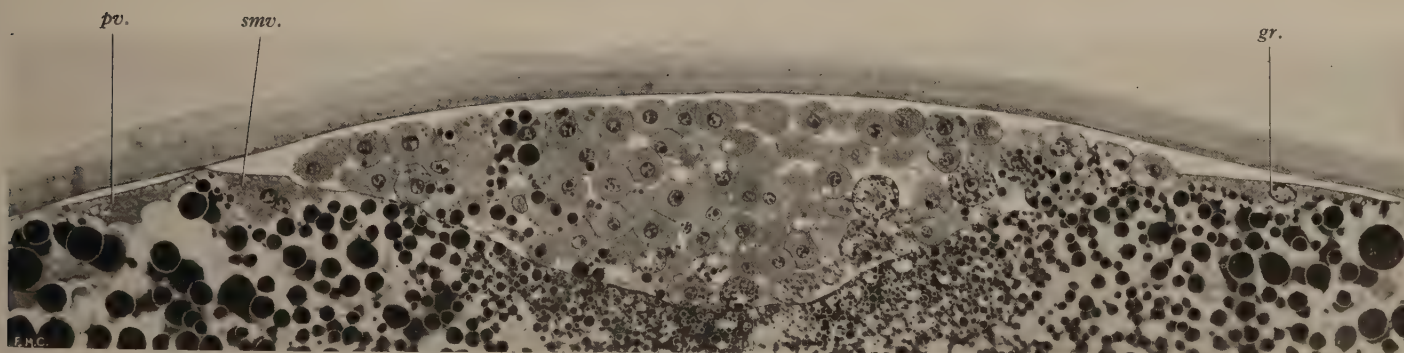
53



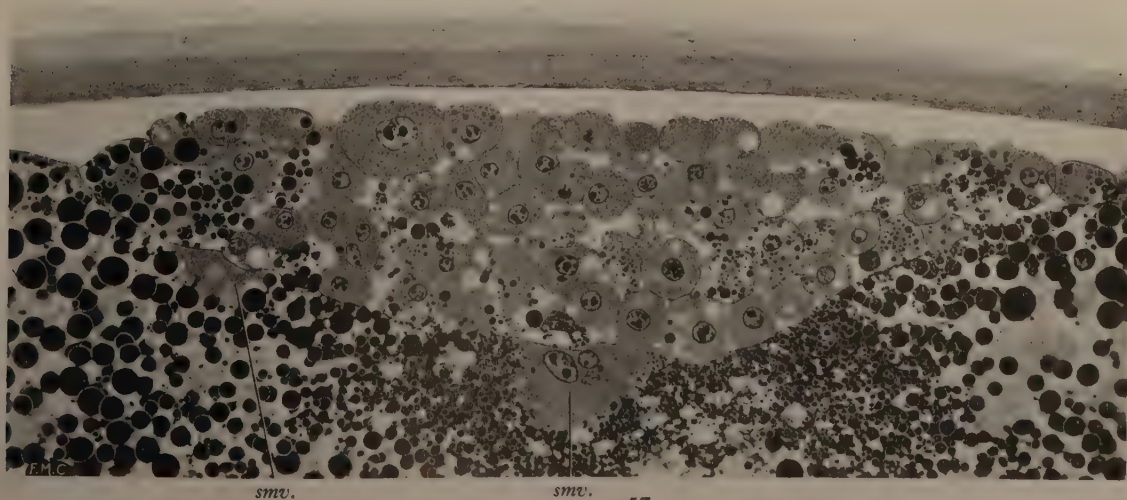
54



55



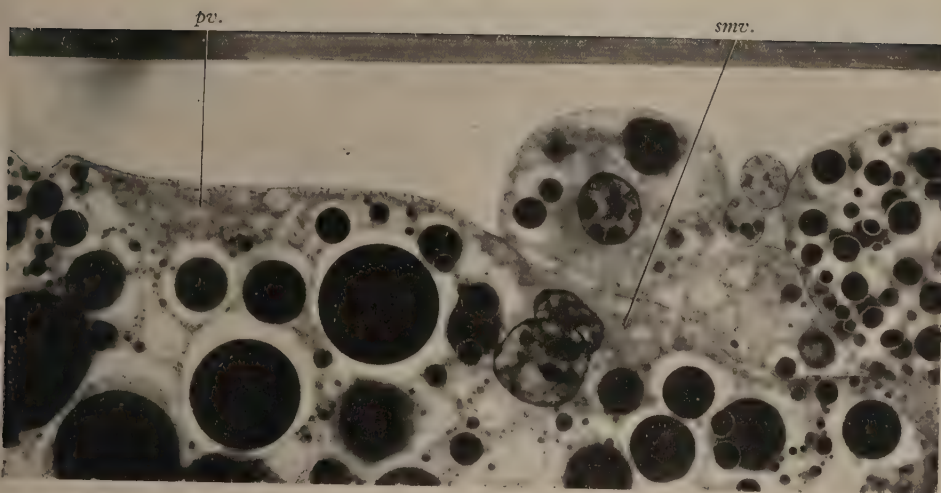
56



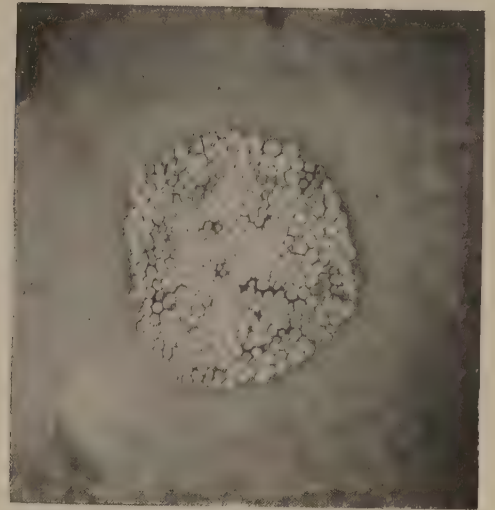
57



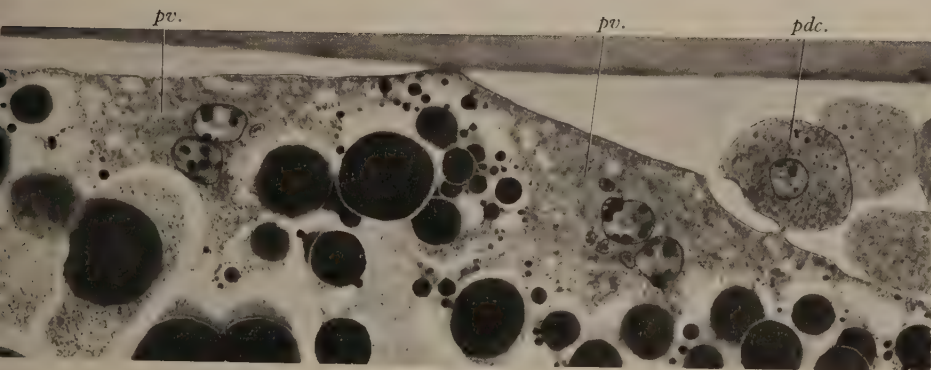




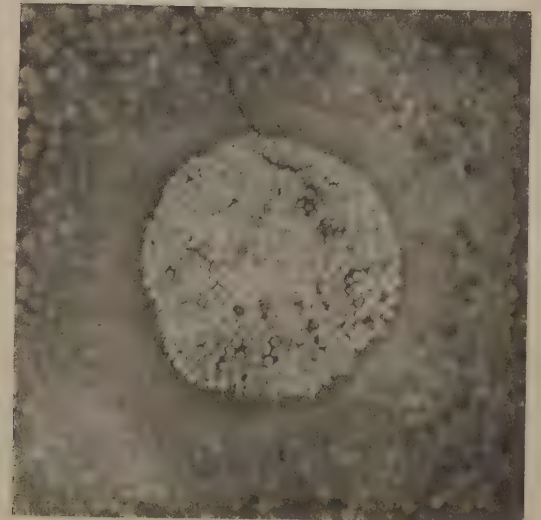
58



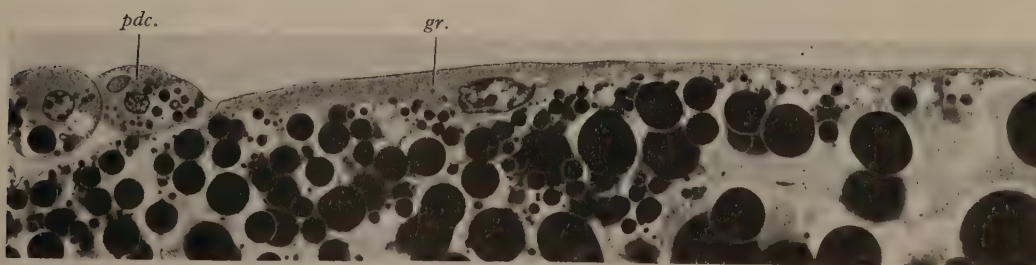
62



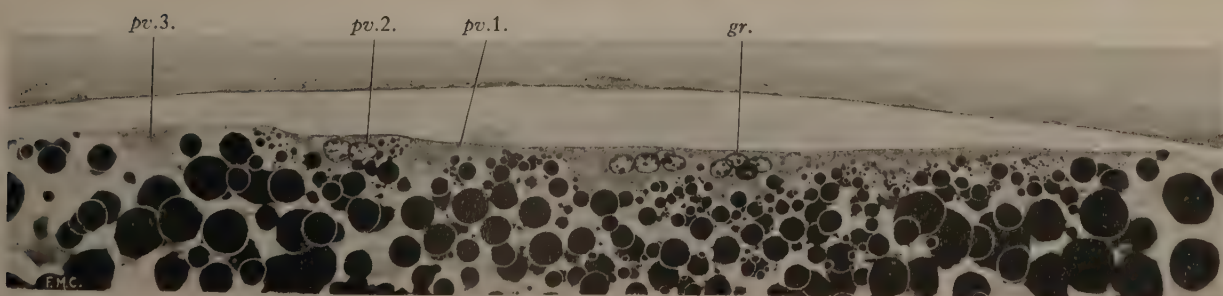
59



64



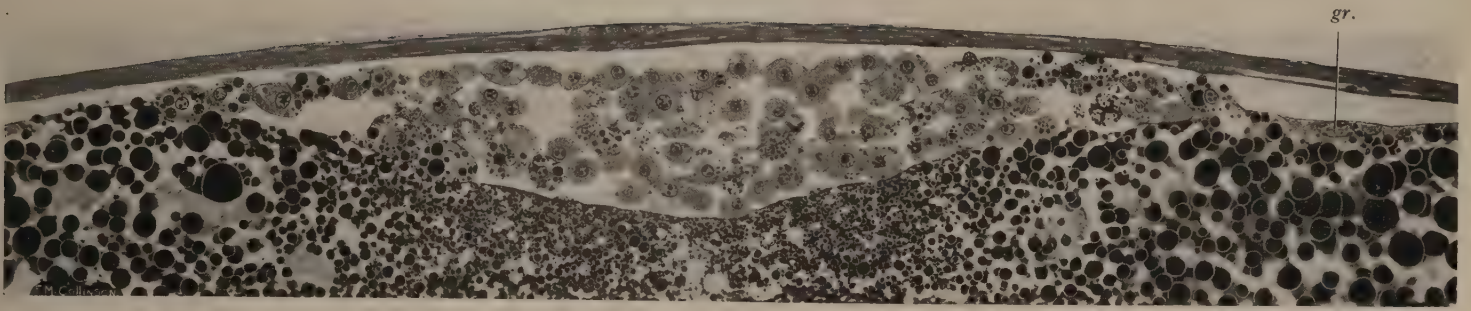
60



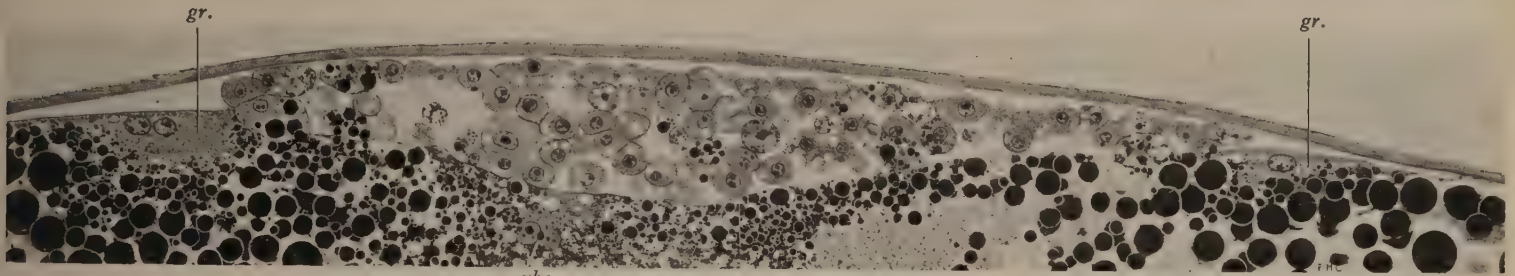
61



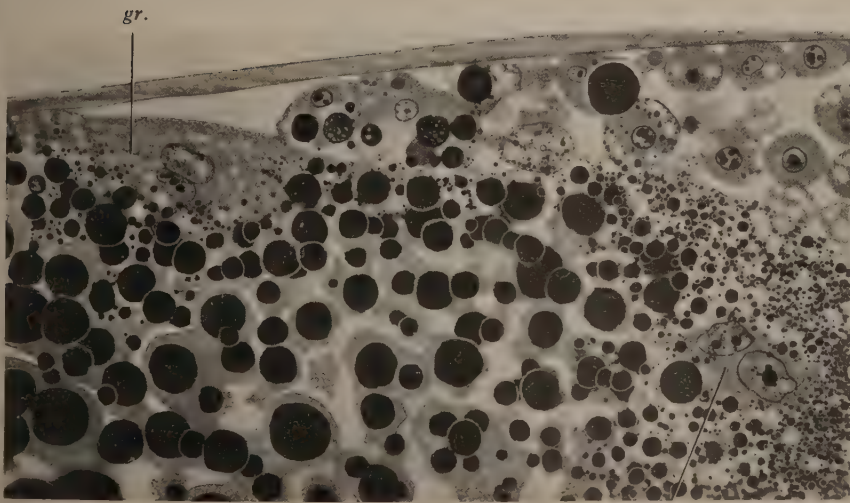




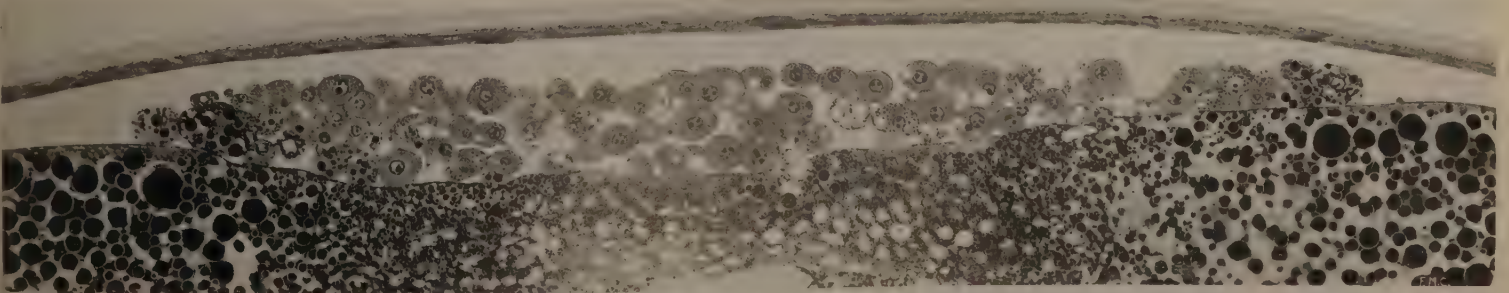
63



65

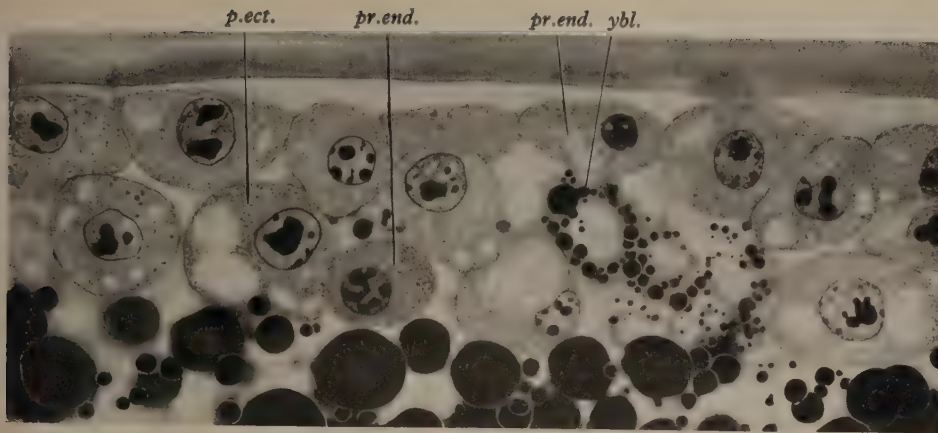


66

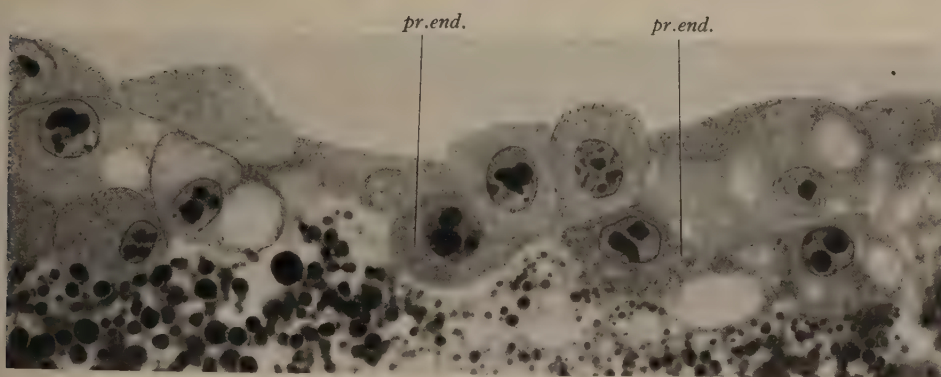




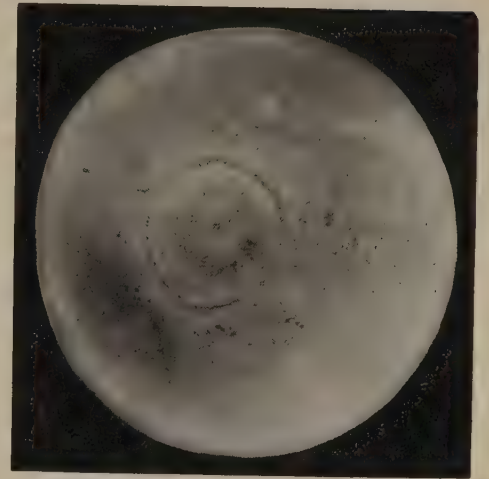




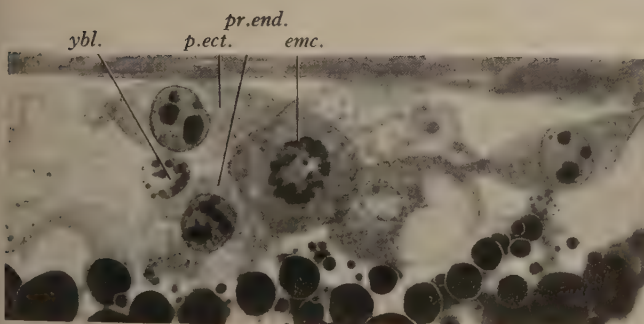
70



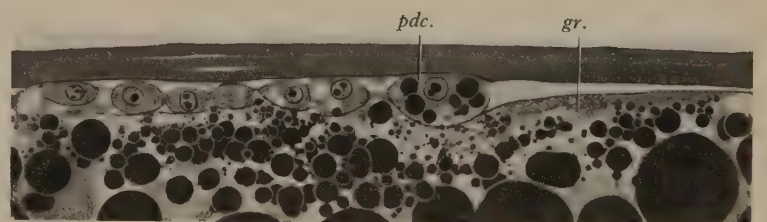
71



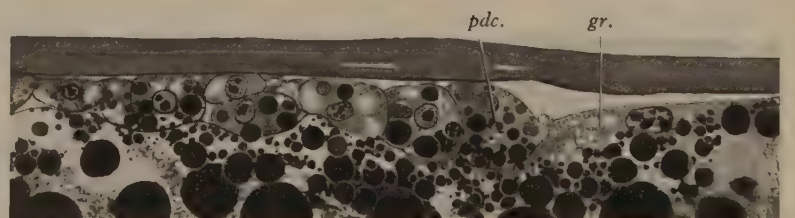
69



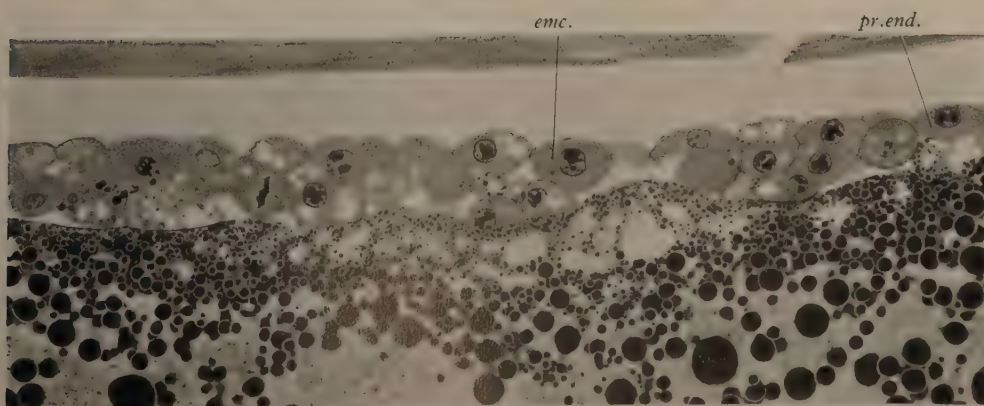
72



73



74



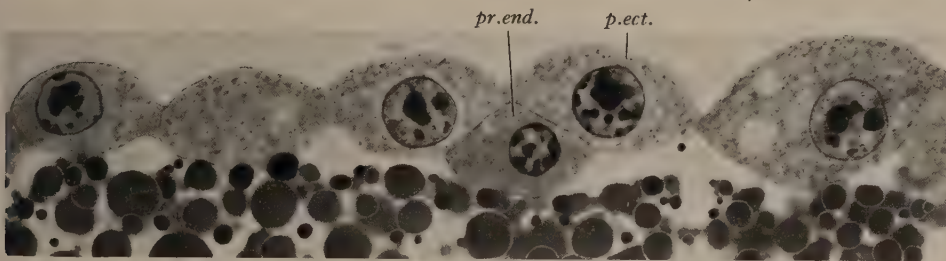
77



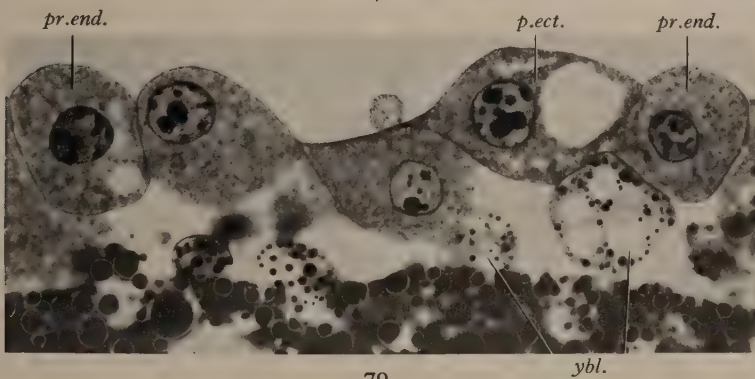




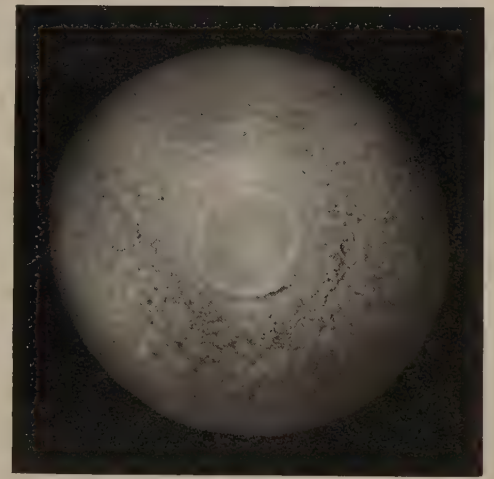
76



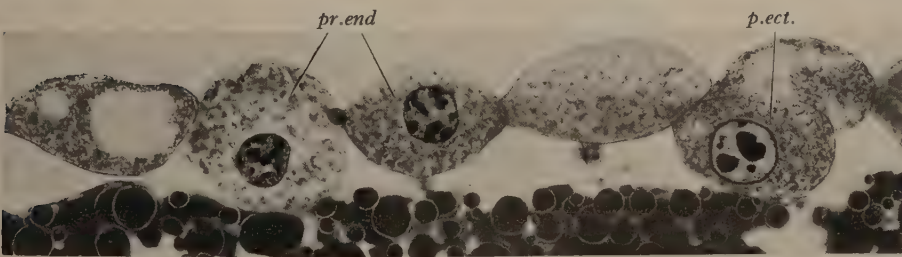
78



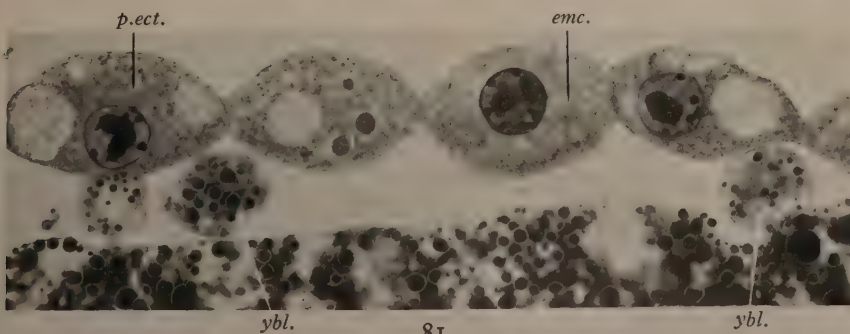
79



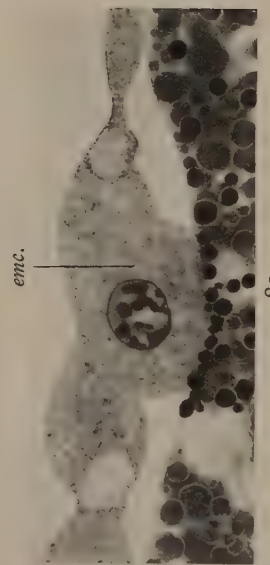
75



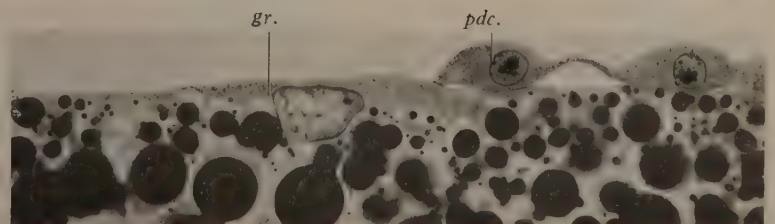
80



81



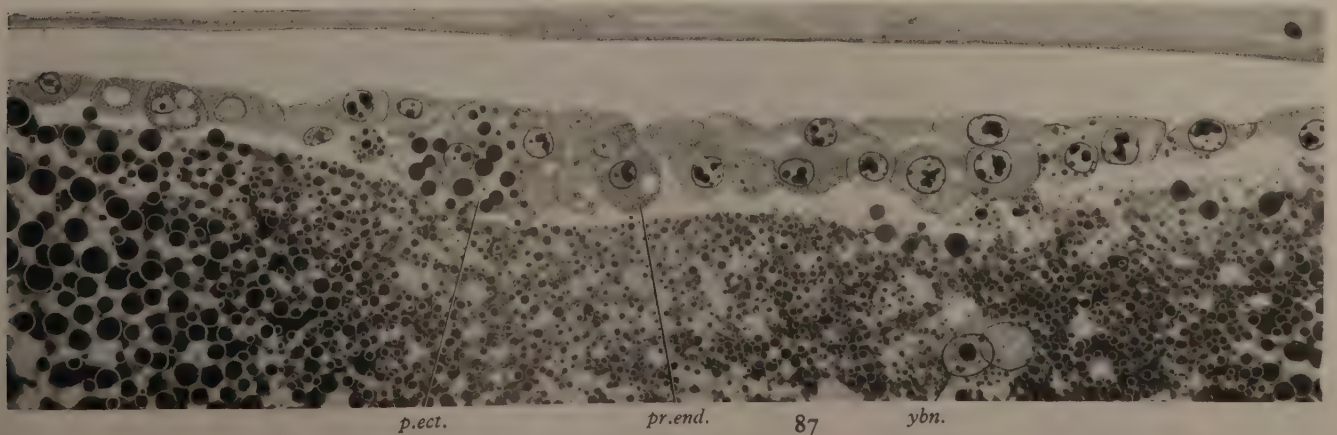
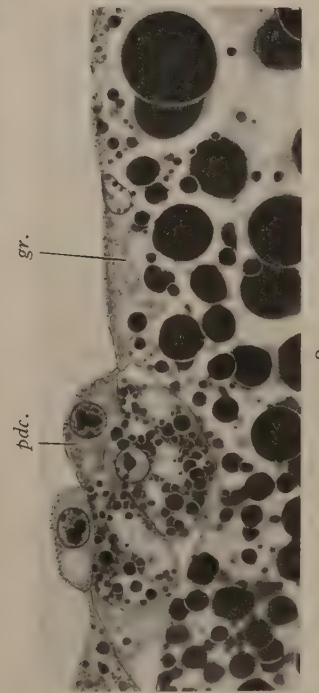
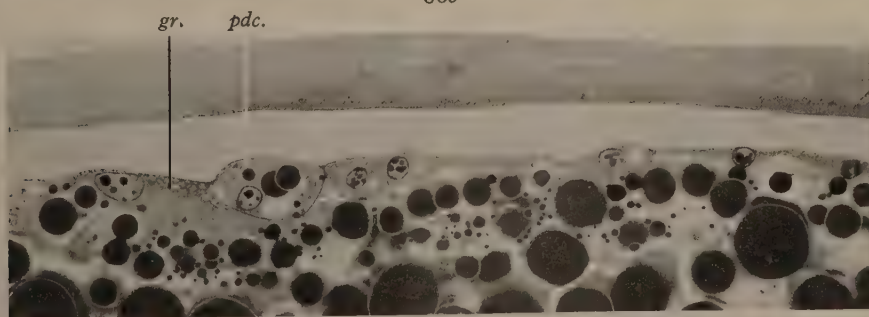
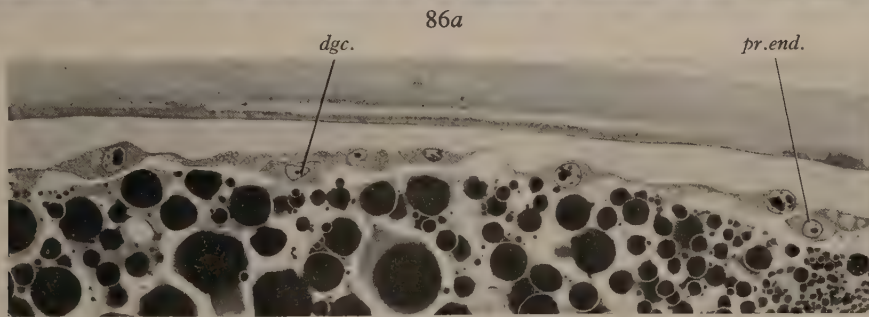
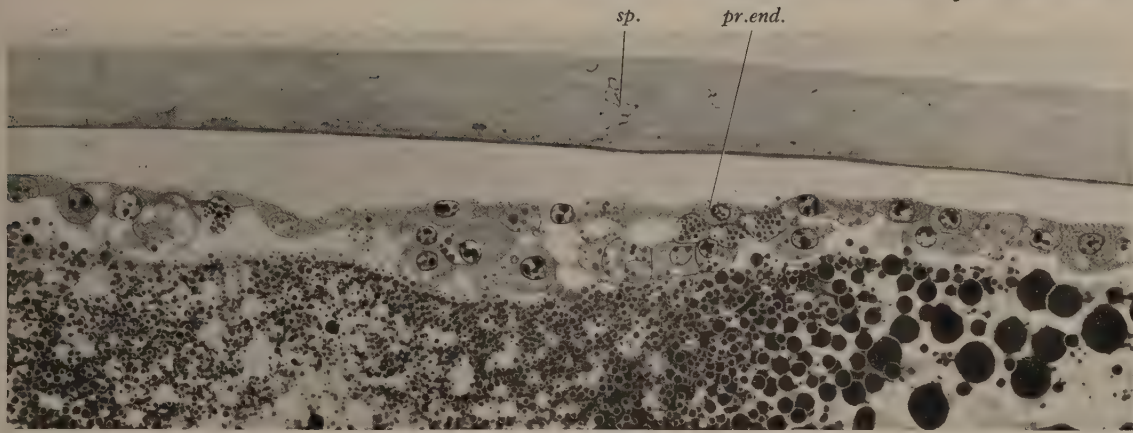
82



83

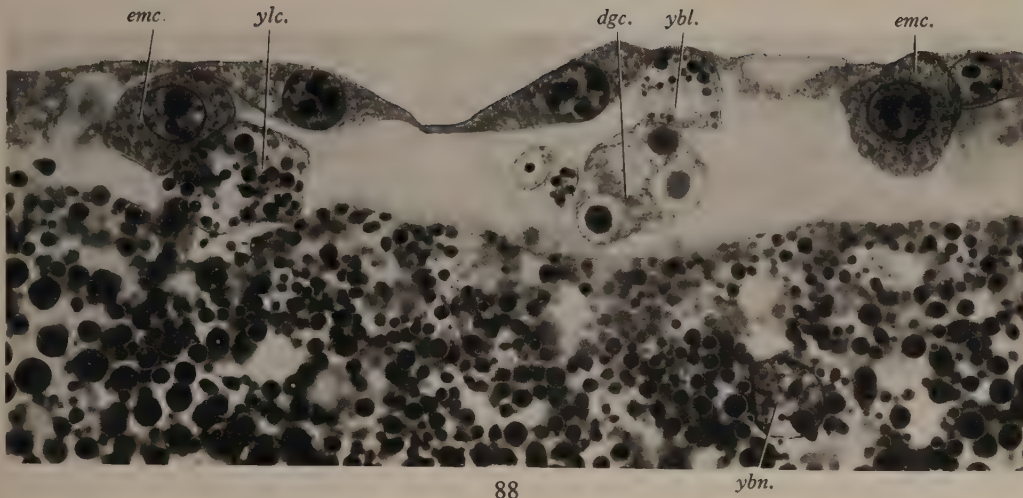




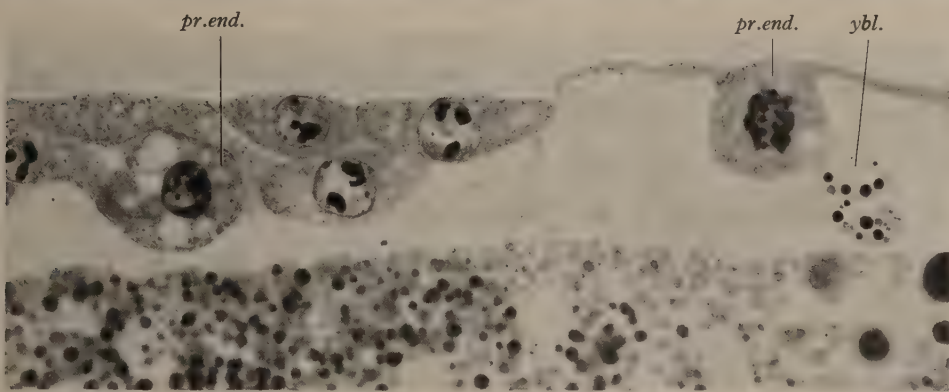




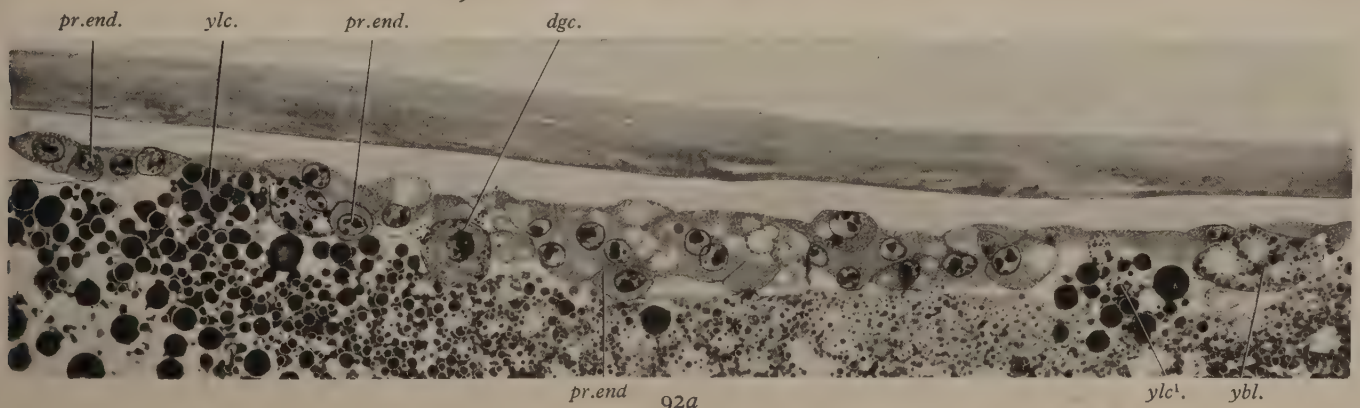




88

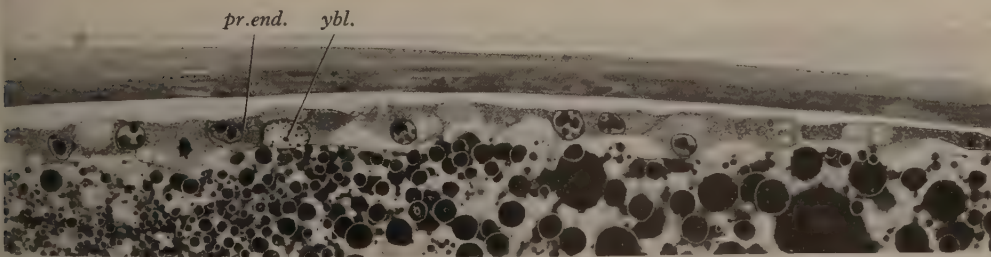


89

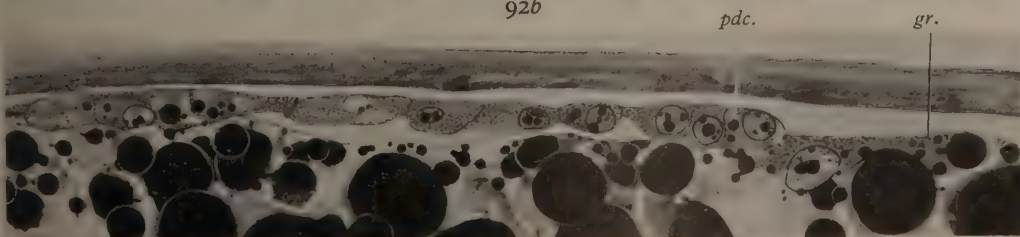


pr.end 92a

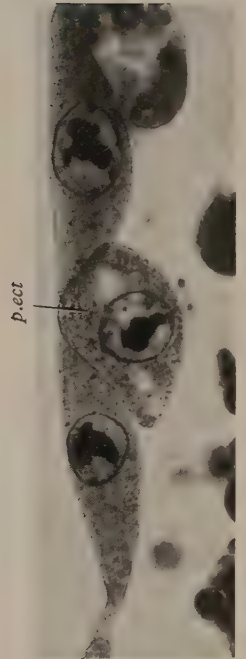
ylc' ybl.



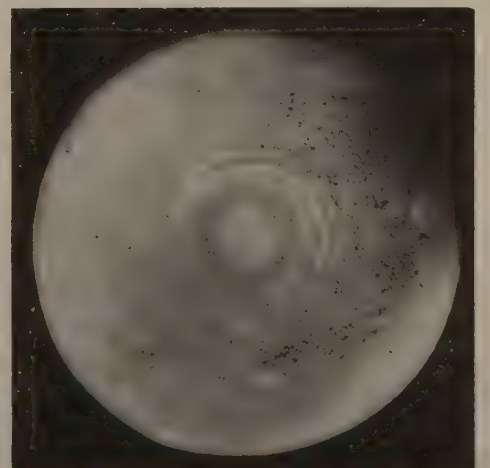
92b



92c



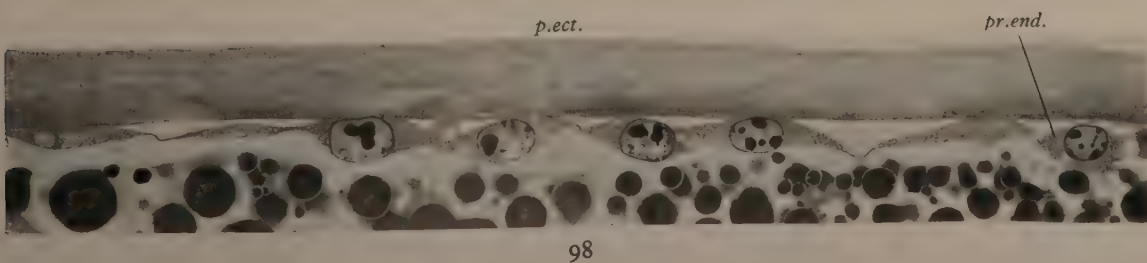
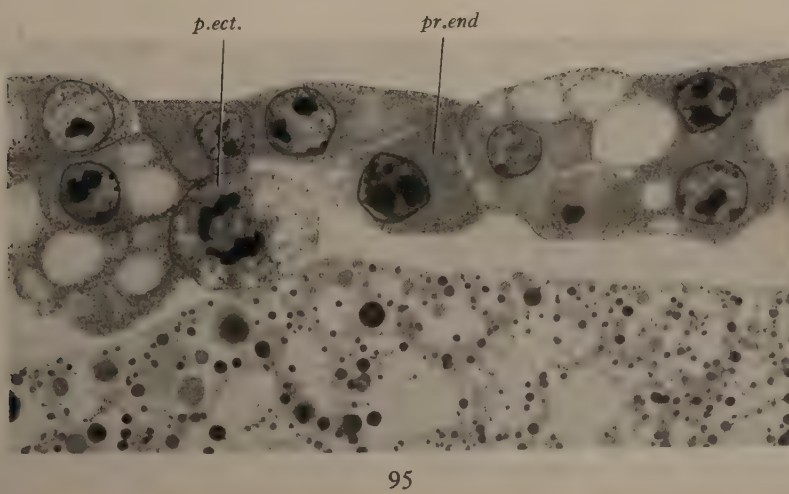
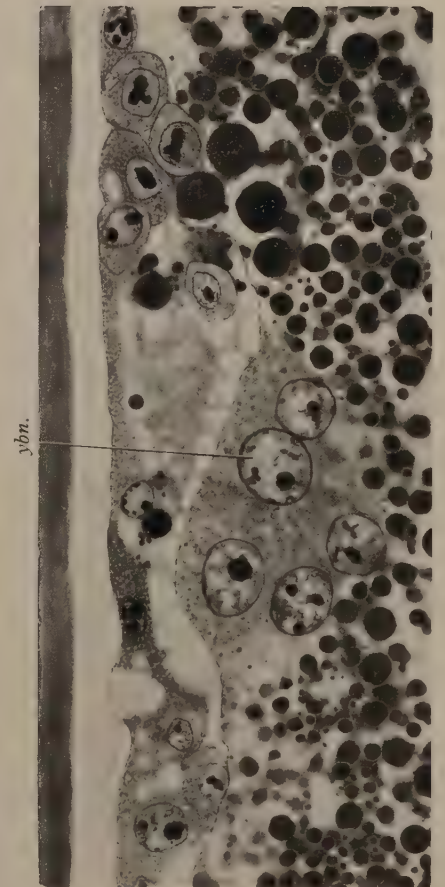
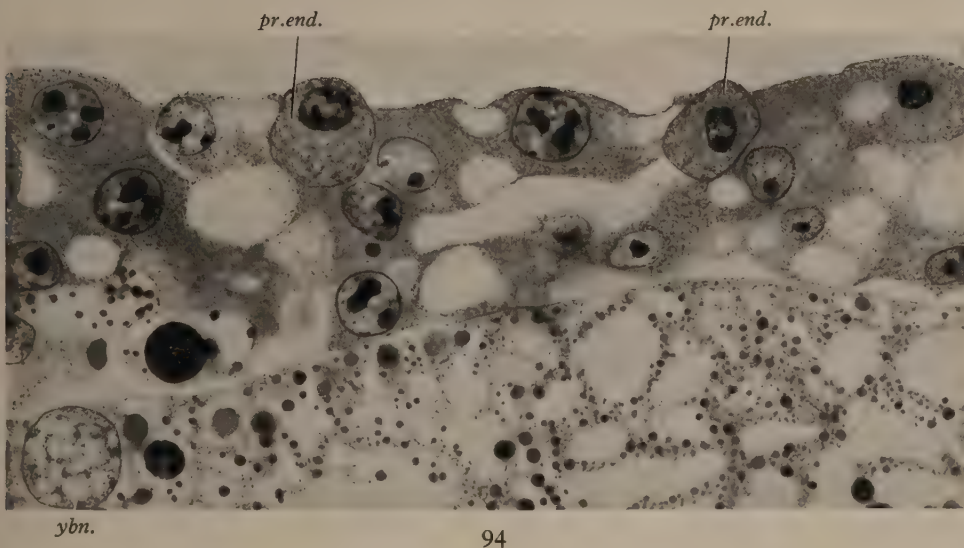
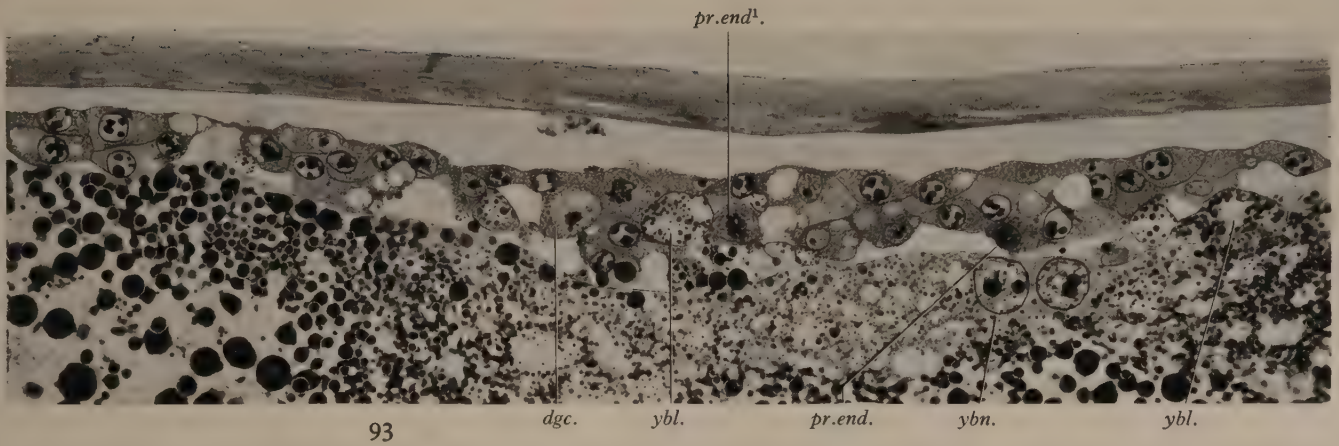
90



91

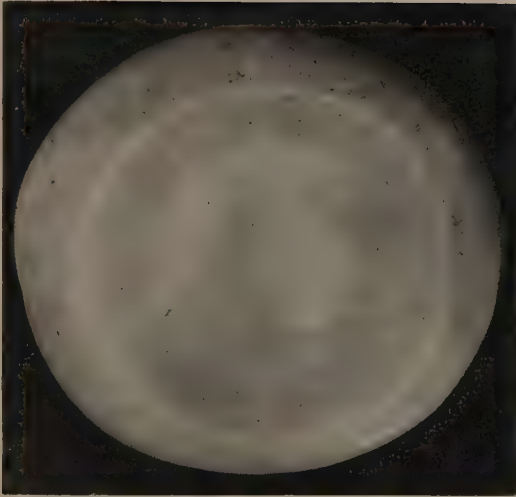




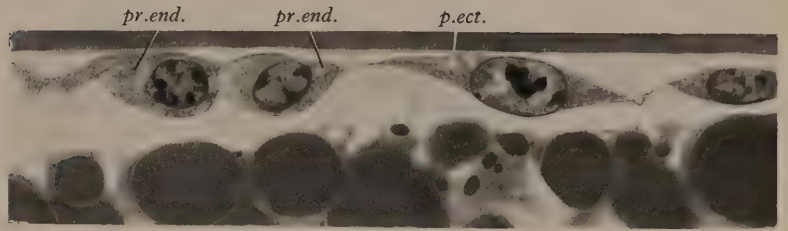








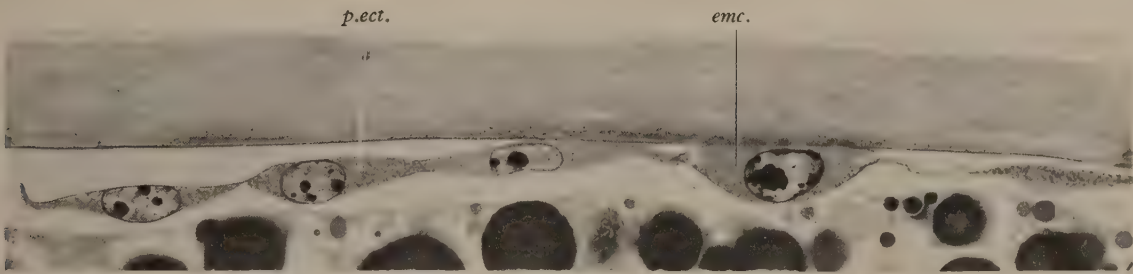
97



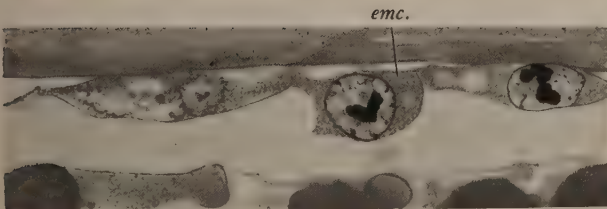
100



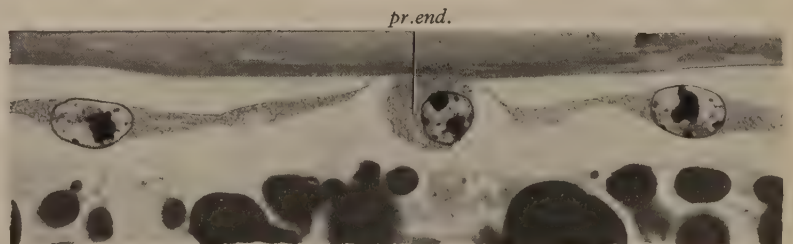
103



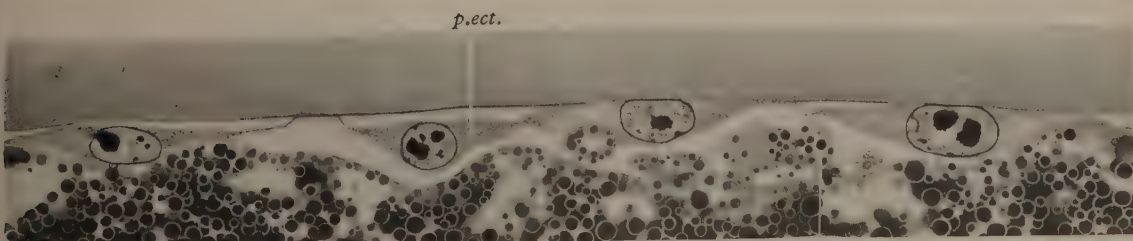
99



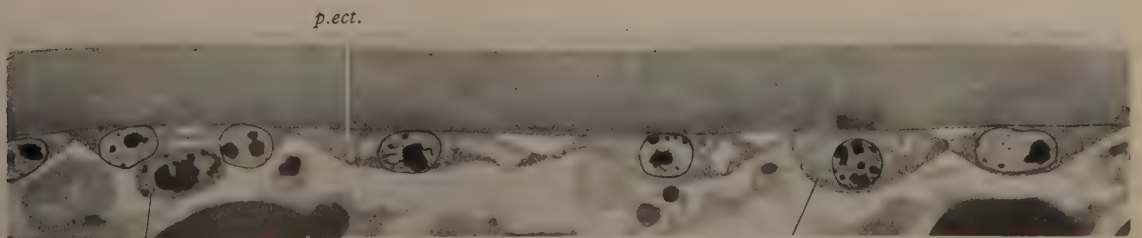
101



102



104

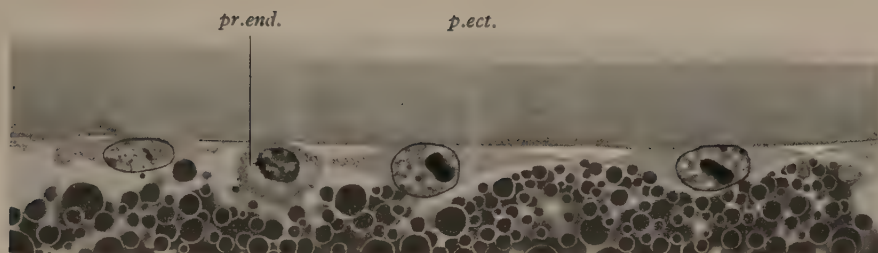


105

pr.end.



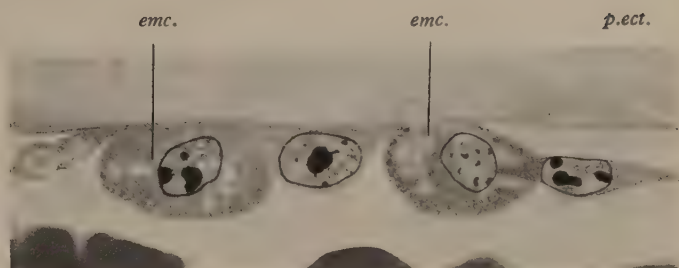




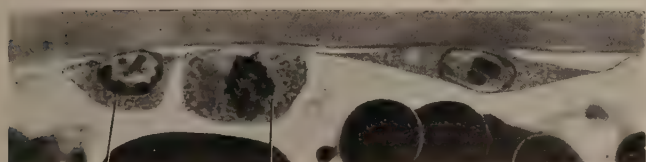
106



107



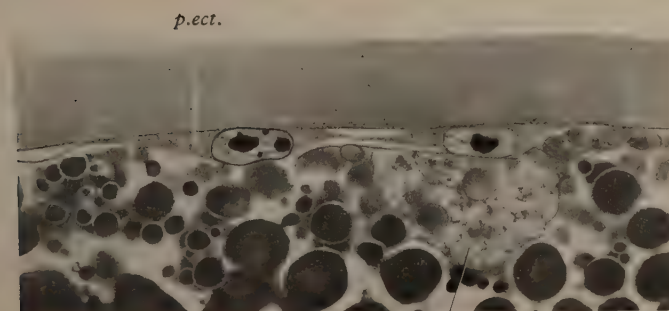
108



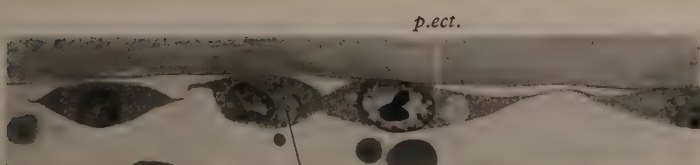
109



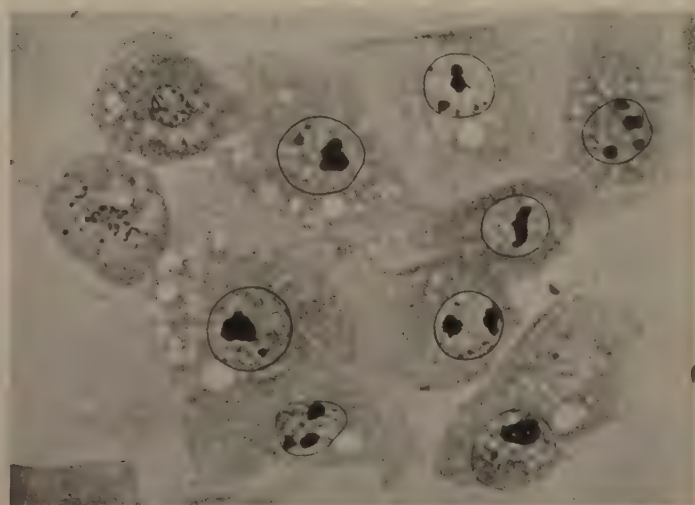
110



111



113



114



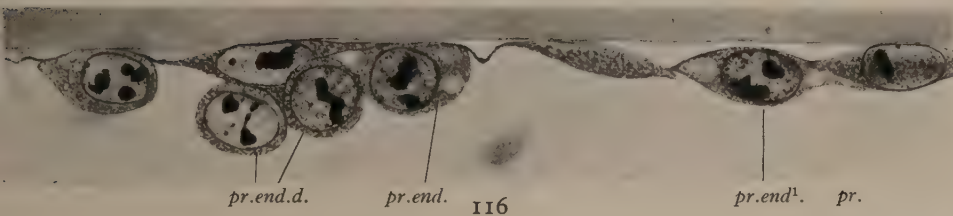
112



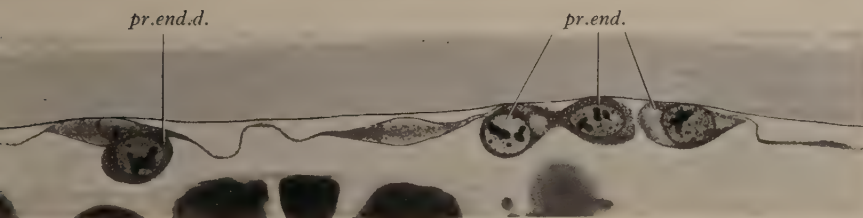




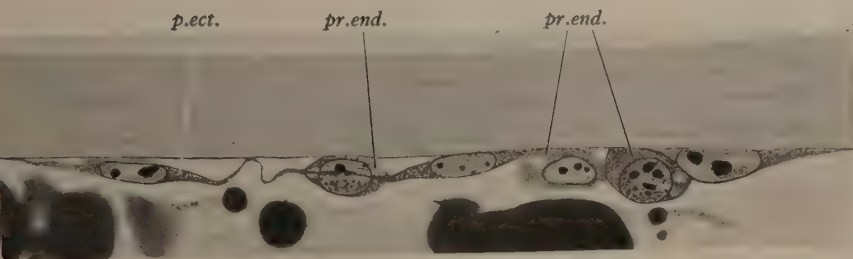
115



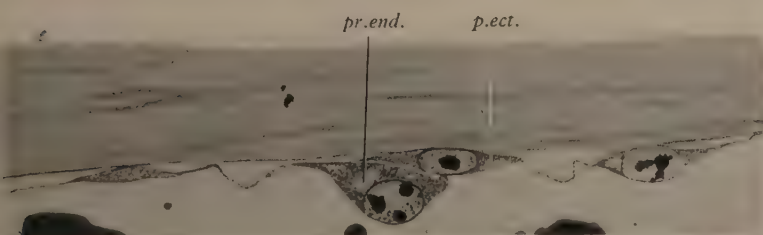
116



117



118



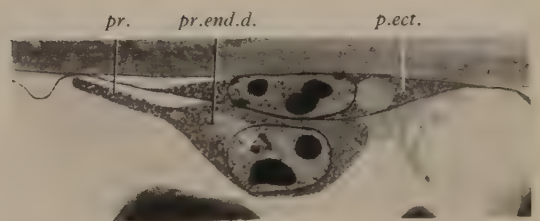
119



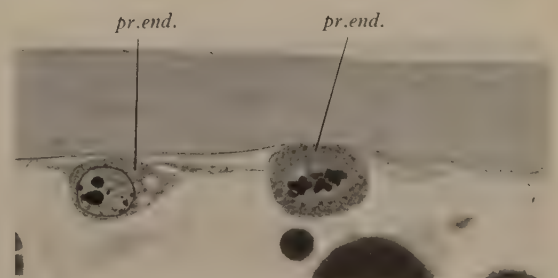
123



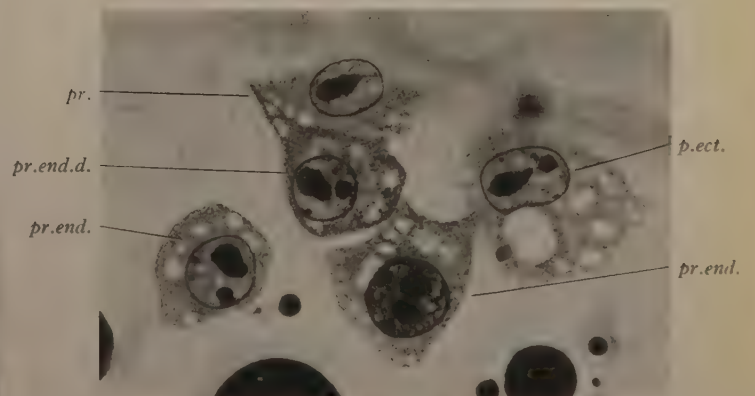
120



121



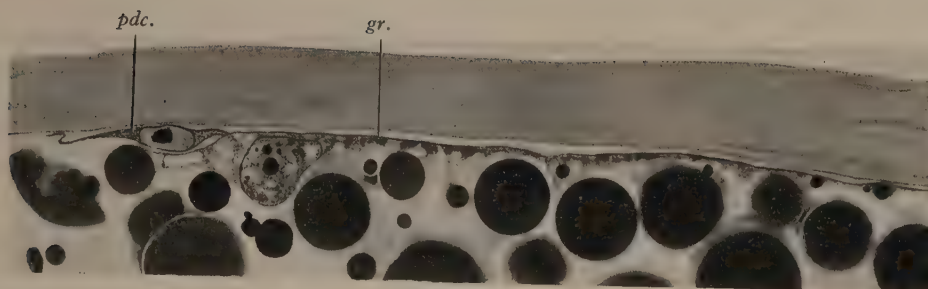
122



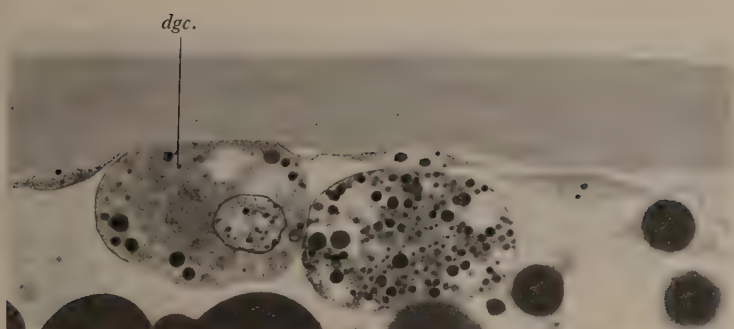
124



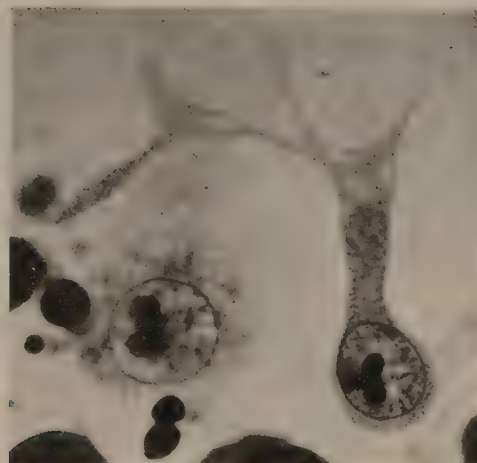




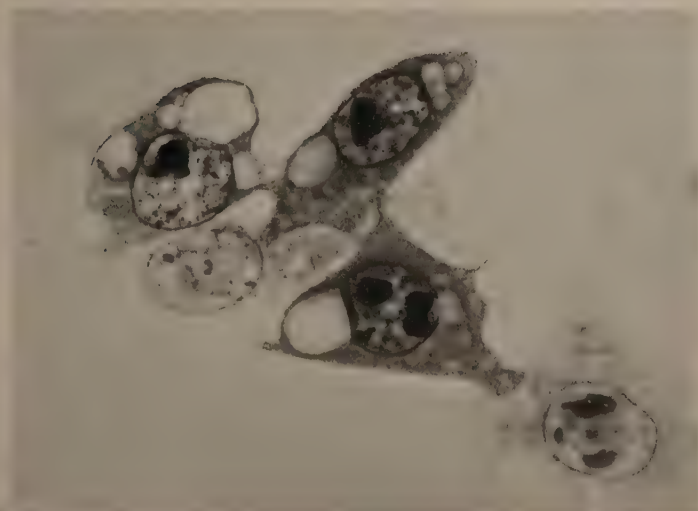
126



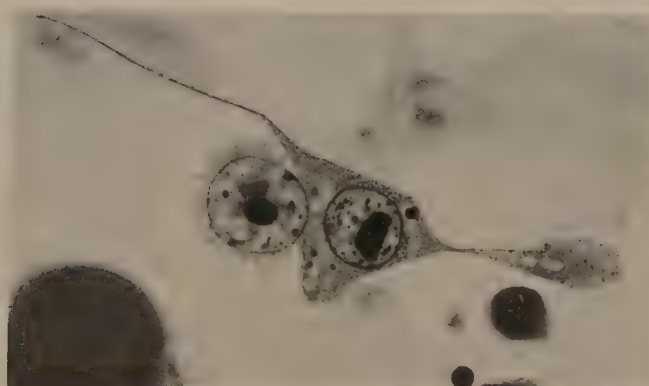
125



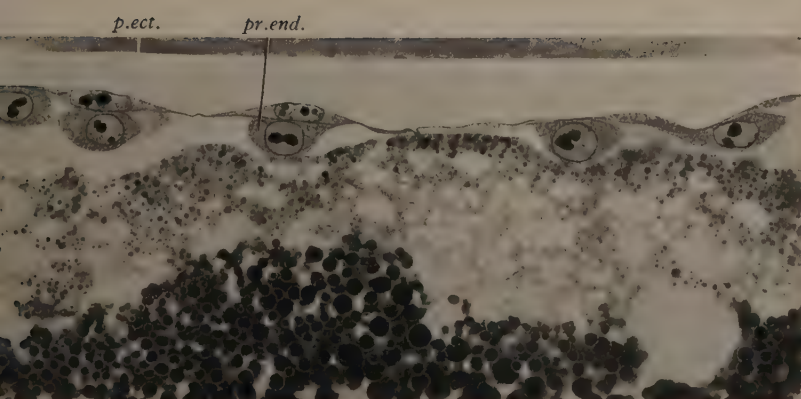
128



127



129



130

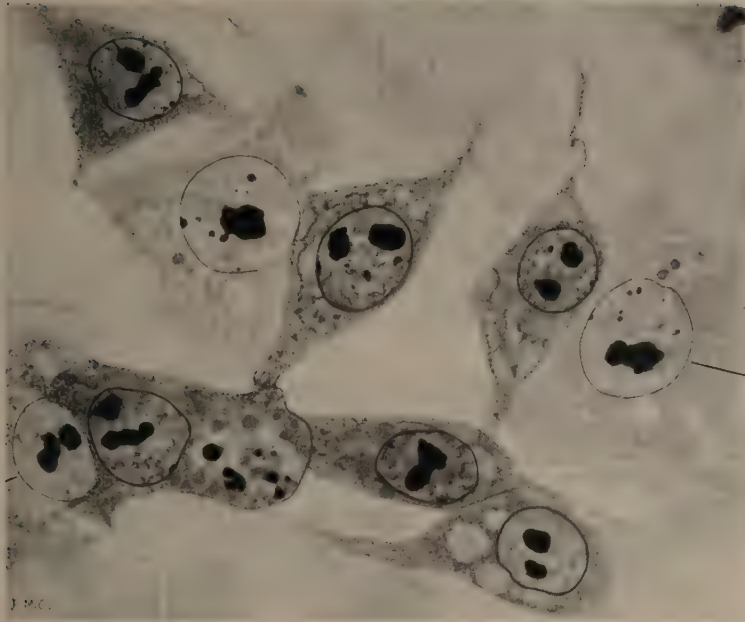


132





2



4

133

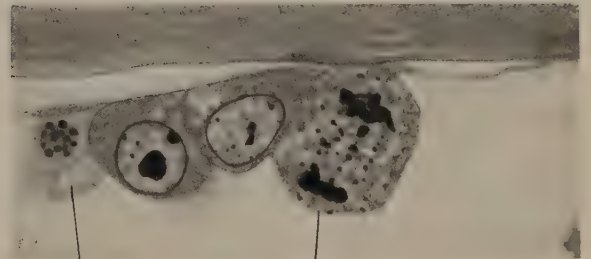
6

3



131

5



139

pr.end.

1

2

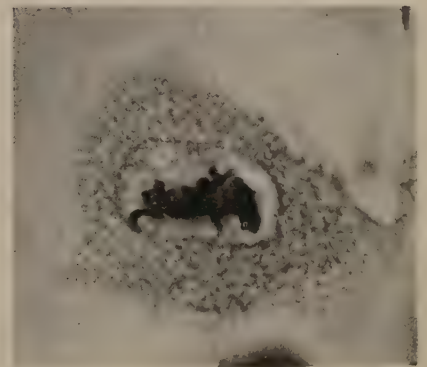
134

3

pr.end.

pr.end.

4



141

p.ect.

pr.

140

pr.end.

135

p.ect.

sc.

p.ect.

pr.end.

pr.

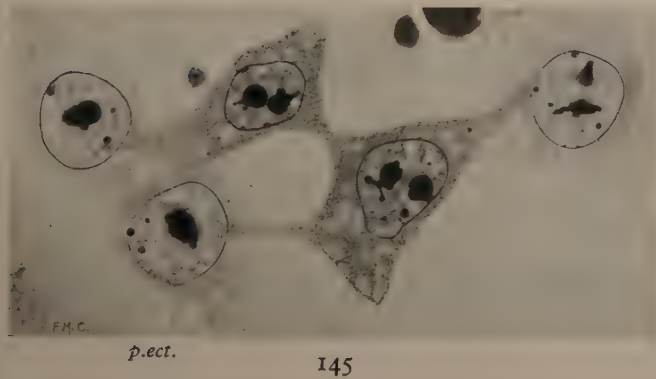
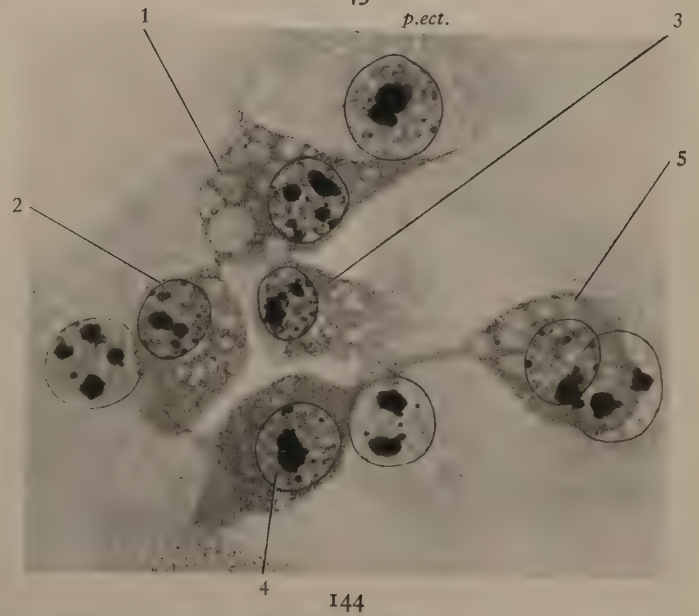
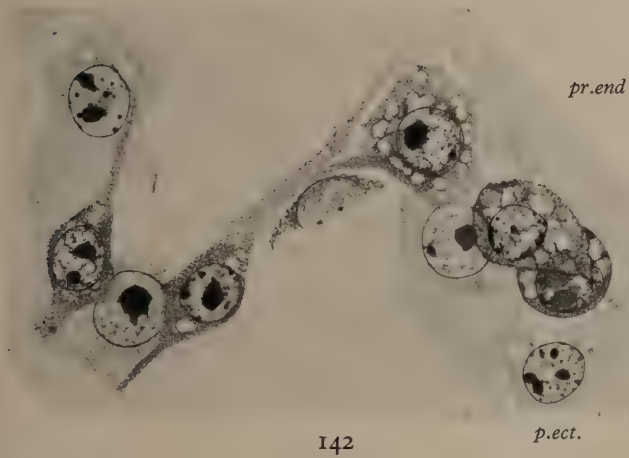
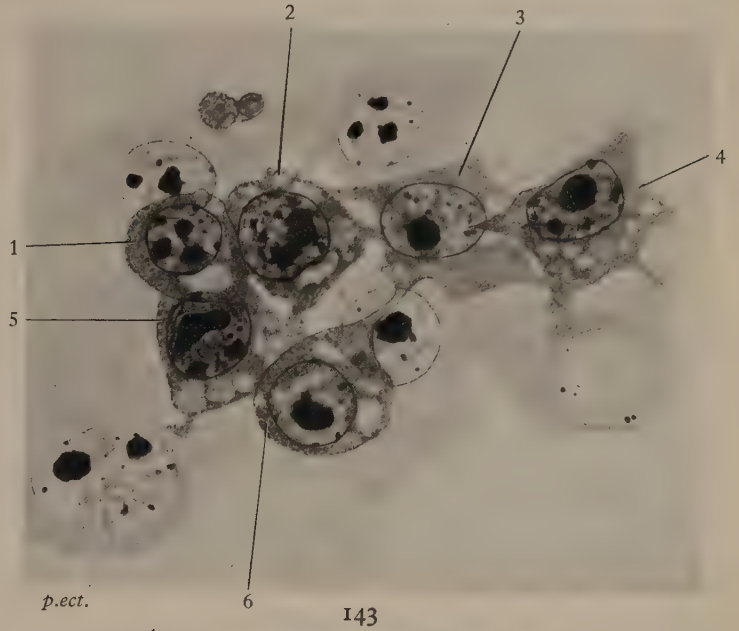
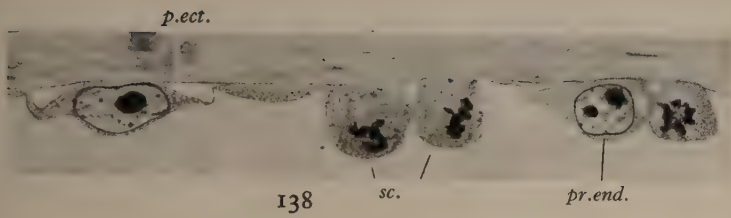
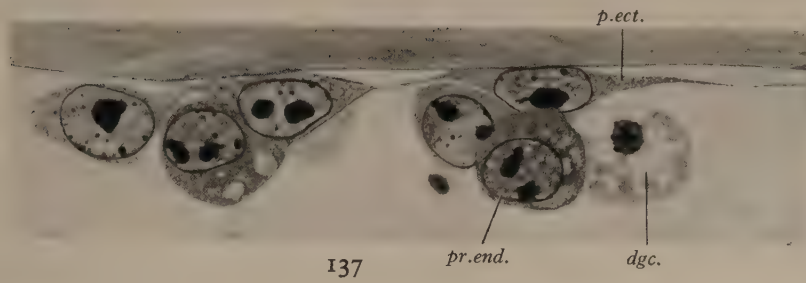
136

dgc.

pr.end.

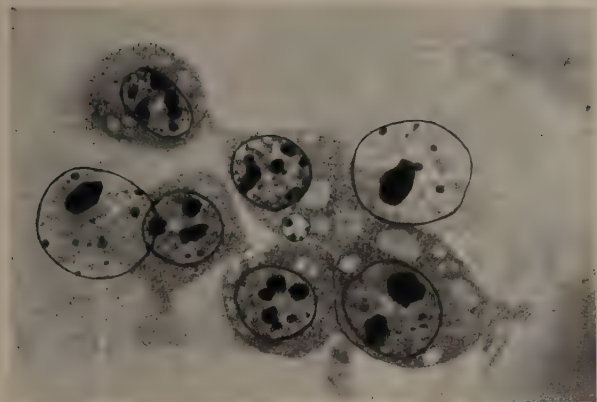






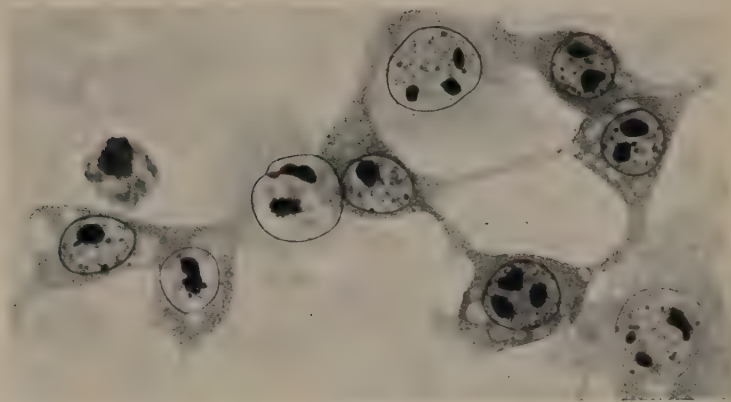






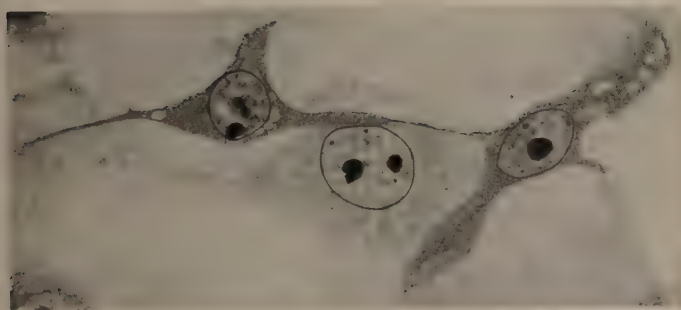
*p.ect.*

147

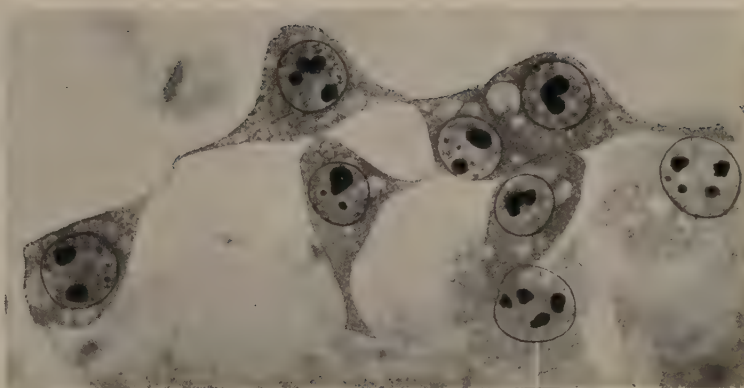


*p.ect.*

148

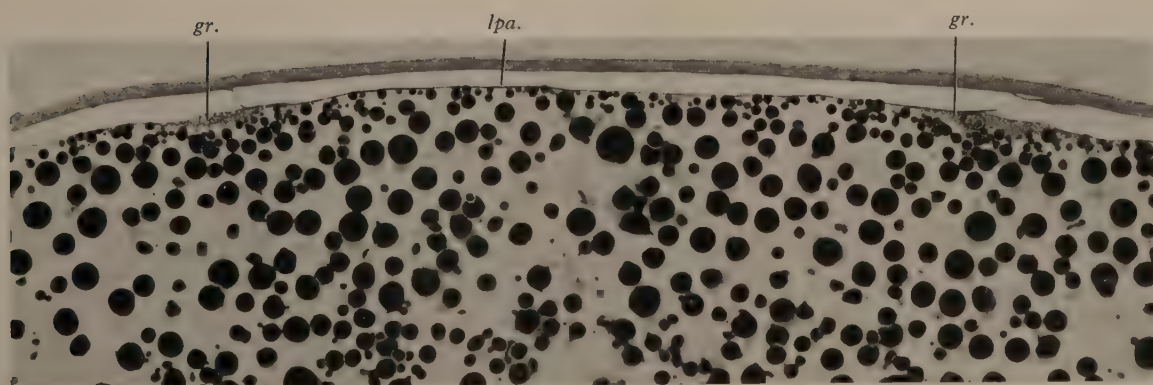


149

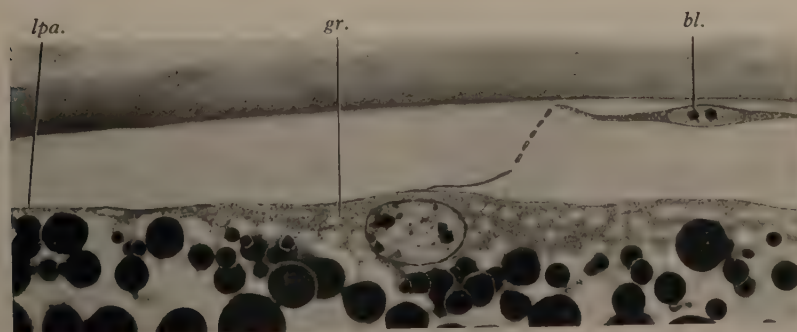


*p.ect.*

150



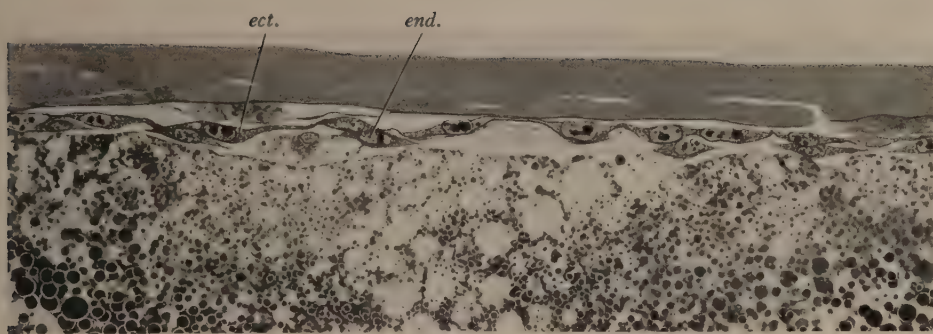
151



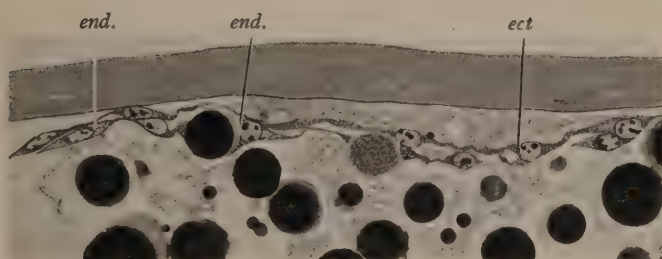
152



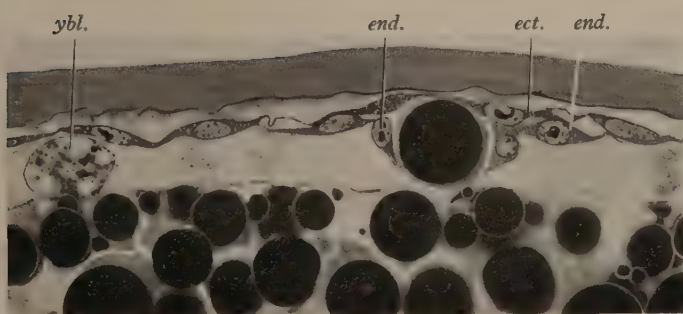




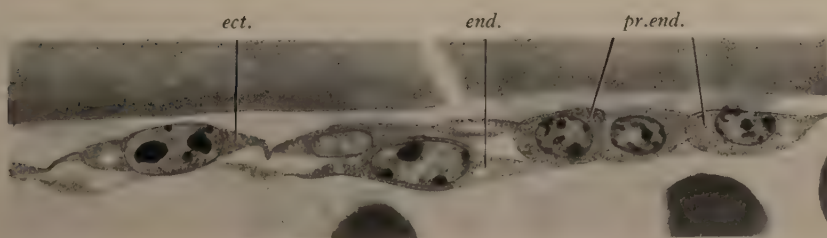
153



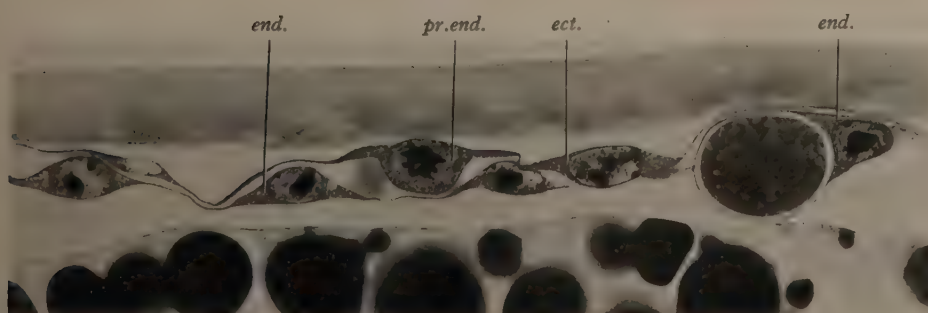
154



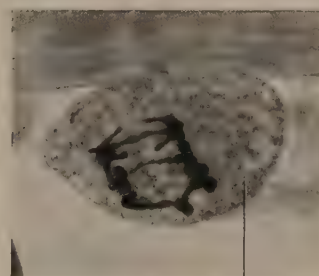
155



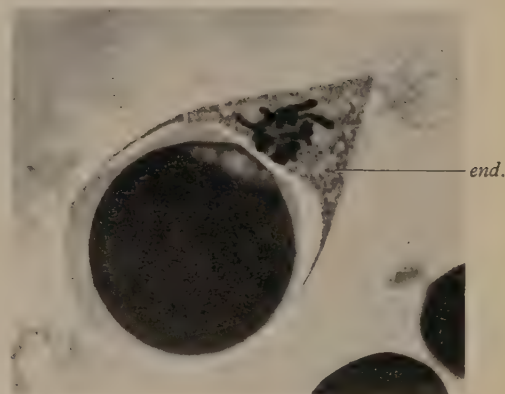
156



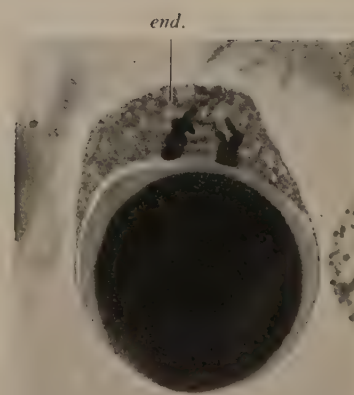
157



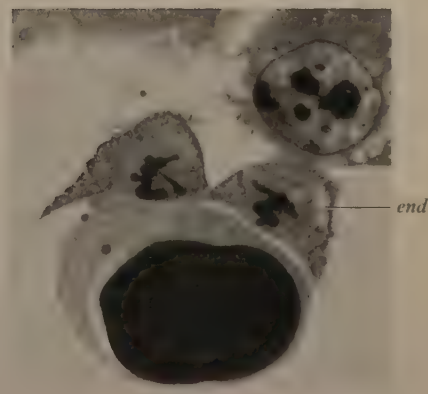
158



159



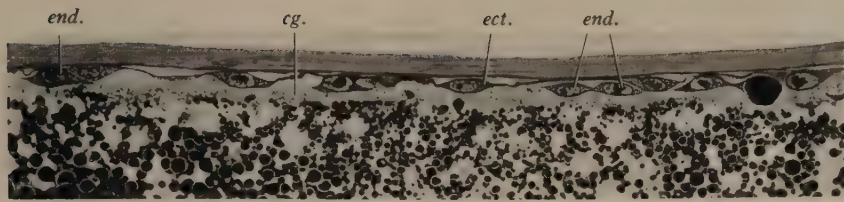
160



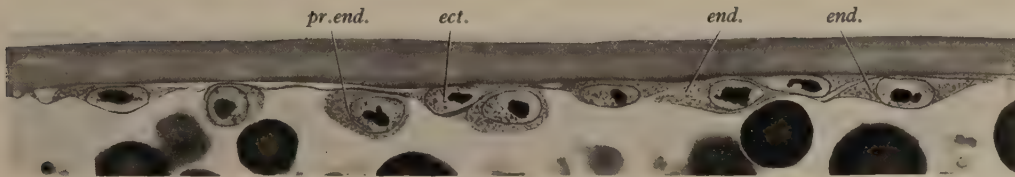
161



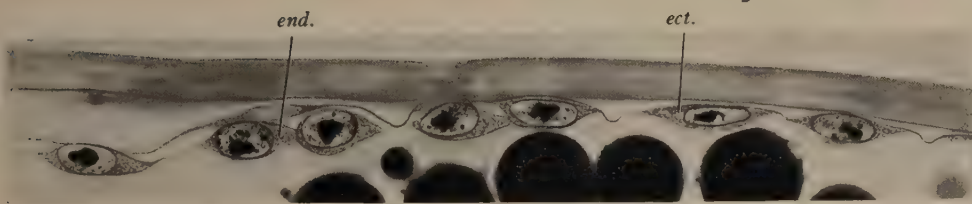




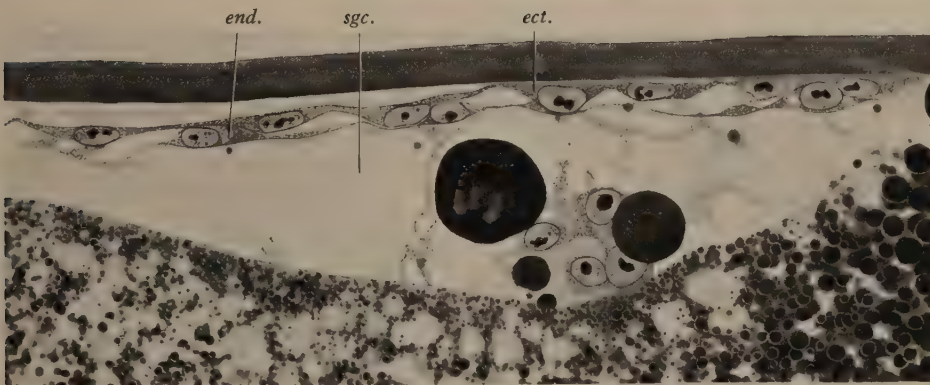
162



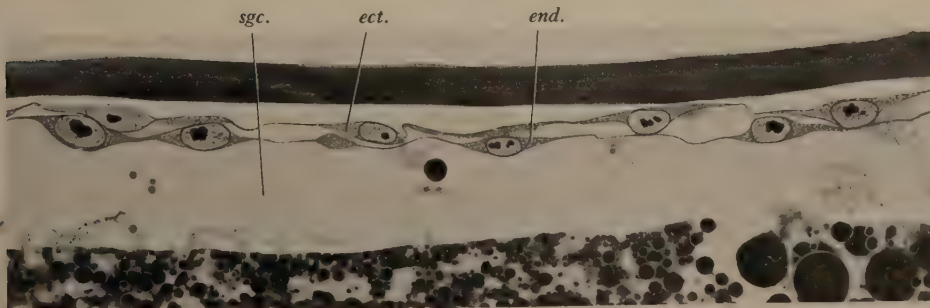
163



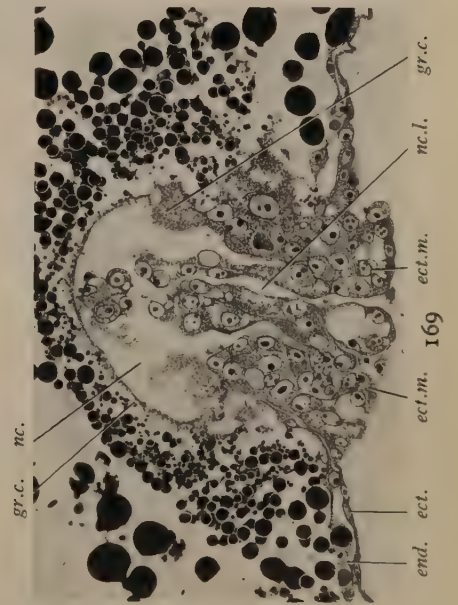
164



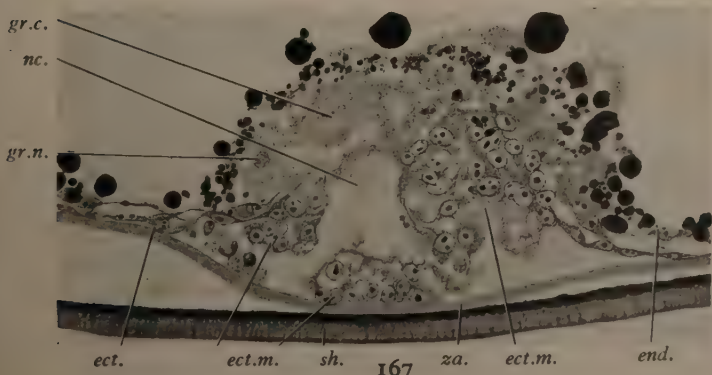
165



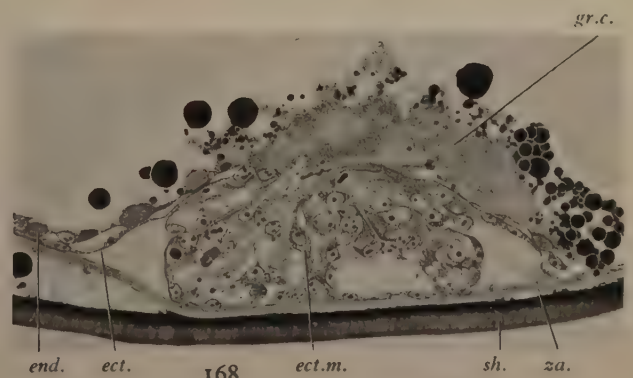
166



169



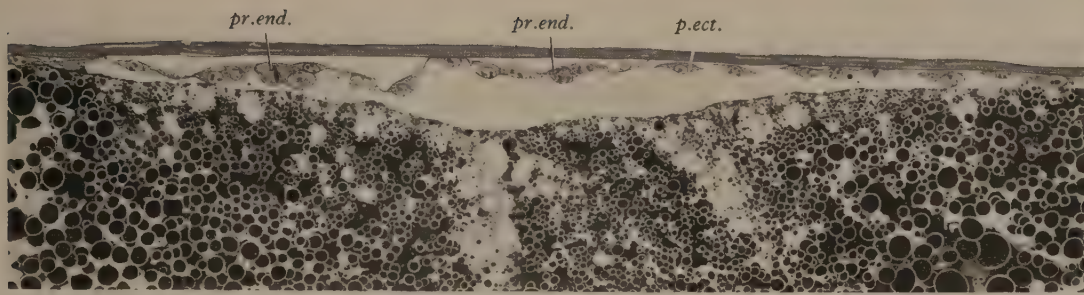
167



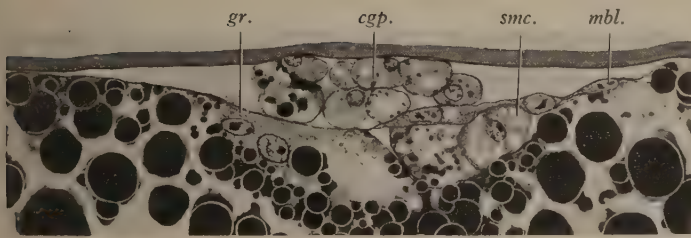
168



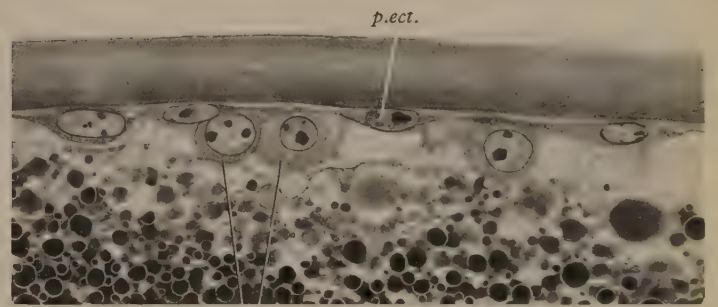




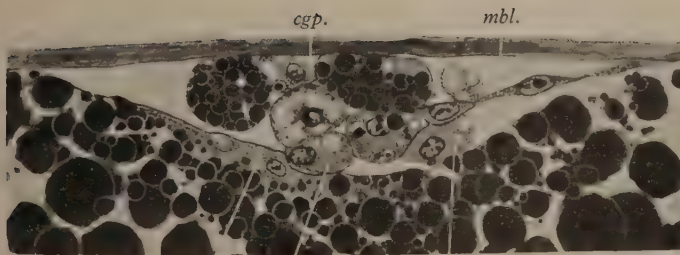
170



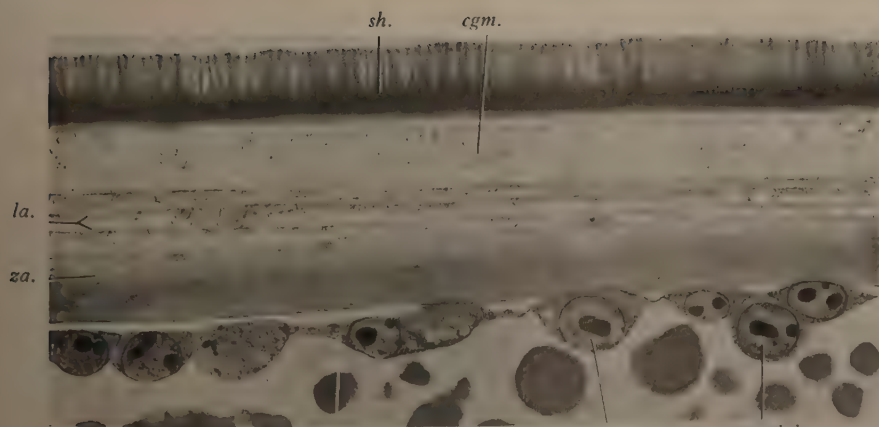
171



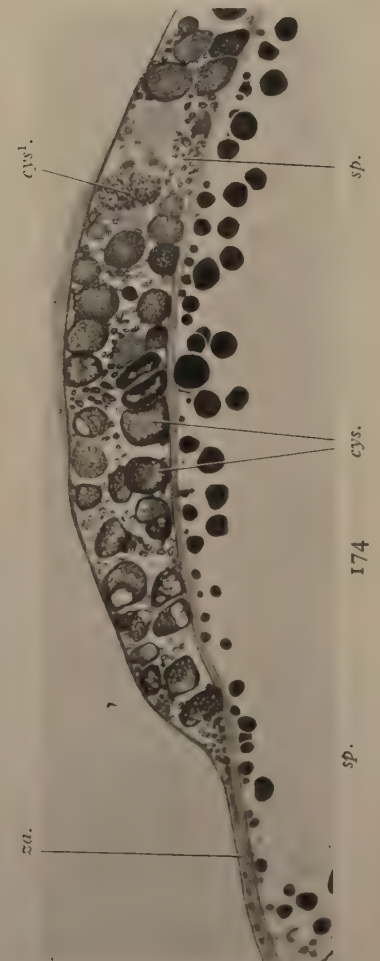
173



172



175



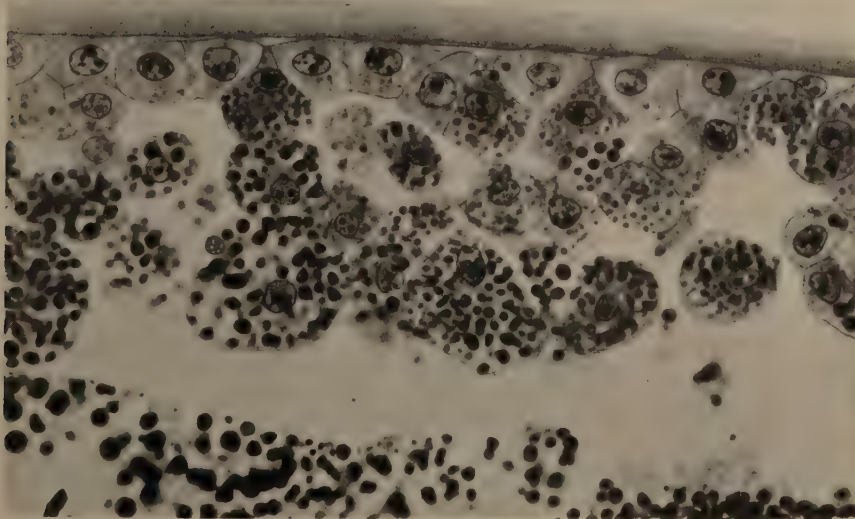
174



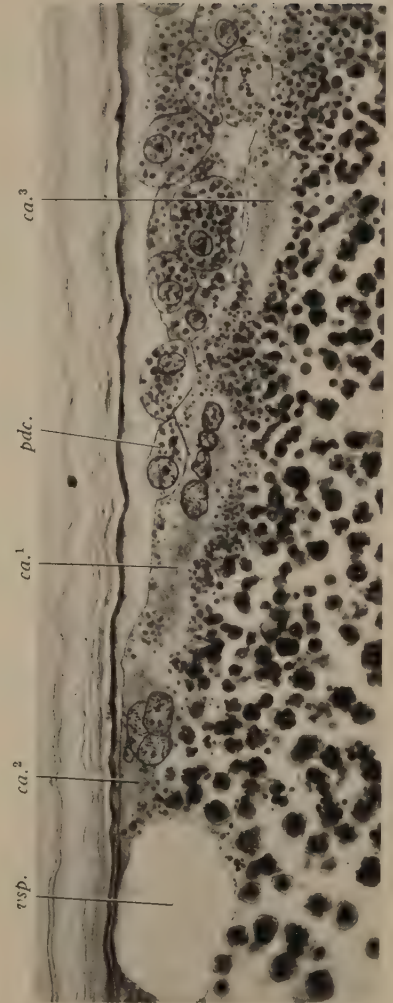




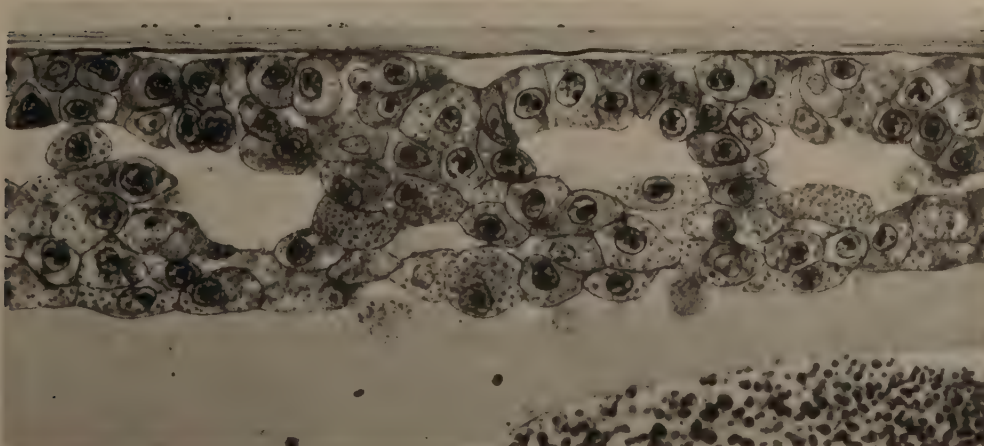
176



177



179



178





*Description of Prosqualodon davidi* Flynn, a Fossil Cetacean from Tasmania. By Professor T. THOMSON FLYNN, Queen's University, Belfast. With a note on the Microscopic Tooth Structure. By J. THORNTON CARTER.

(PLATES I-VI, and Text-figures 1-11.)

[Received March 2nd, 1948.]

# CONTENTS.

	Page
I. HISTORICAL ACCOUNT OF THE GENUS <i>PROSQUALODON</i> .....	153
II. DESCRIPTION OF <i>PROSQUALODON DAVIDI</i> .....	155
(a) Discovery, locality, etc. ....	155
(b) Skull Characters .....	156
(c) Details of Skull Structure .....	157
(d) Dentition .....	169
(e) Pectoral Girdle and Fore-limb .....	175
(f) Sternum .....	178
III. REMARKS ON THE SKULL OF <i>PROSQUALODON AUSTRALIS</i> LYD., IN THE BRITISH MUSEUM..	179
IV. REMARKS ON THE MOLAR TEETH OF <i>PROSQUALODON</i> .....	183
V. THE SYSTEMATIC POSITION OF THE GENUS <i>PROSQUALODON</i> .....	184
VI. AUSTRALASIAN REMAINS OF ARCHAEOCETI AND PRIMITIVE ODONTOCETI .....	185
VII. <i>PROSQUALODON</i> IN ITS RELATION TO CETACEAN PHYLOGENY .....	187
(a) Evidence of Intra-cranial Casts .....	188
(b) Structure of Posterior Region of the Palate .....	188
(c) Microscopical Structure of the Teeth by J. Thornton Carter .....	192
VIII. SUMMARY .....	193
IX. LIST OF REFERENCES .....	193
X. DESCRIPTION OF PLATES .....	196

## I. HISTORICAL ACCOUNT OF THE GENUS *PROSQUALODON*.

(a) In 1893, Lydekker described a new genus of primitive cetacean from the Chubut Beds of Patagonia. This genus, while generally of the squalodont type, was shown by Lydekker to differ from that type in a number of points, especially in the form of the nasals and in the length of the rostrum. Lydekker's description is very short and no measurements are given. Of this specimen, *Prosqualodon australis*, the material consisted of a fairly well preserved skull and a portion of the right \* mandible containing three molar teeth. This type material is now in the Museum of La Plata.

(b) Some years later (Lydekker, 1899) there was acquired by the Natural History Museum a similar, perhaps more perfect, skull from the same deposit which was referred by Lydekker to the same genus and species. This skull is now in the Natural History Museum (M 7249). With the skull are a portion of the left † mandible and a "detached" tooth to which reference will be made later.

\* Lydekker calls this mandible the "left" and shows it in the wrong position in his figures (1893, pl. iv, figs. 1 & 1 a).

† Lydekker calls this mandible the "right".



With this skull, registered as M 7249 and M 7253-7, are some vertebrae, an atlas, several axes, earbones and bones of the arm and hand, all from Chubut, received apparently about the same time as the skull and doubtfully referred to *Prosqualodon australis*. With these it is not proposed to deal in the present communication.

(c) In 1908, Stromer suggested that, taking into consideration its organization and its geological age, a more appropriate name for this genus would be "*Postsqualodon*".

(d) A portion of a right lower ramus, a number of teeth, some vertebrae, and a periotic from Santa Cruz territory, formed the basis of a contribution by True in 1910 and by him were referred to *Prosqualodon australis*.

(e) The whole question of the status of the genus *Prosqualodon* was considered in detail by Abel (1912), who travelled to London for the purpose of examining the skull in the British Museum. As a result he gave a full description of the features of this skull as he conceived them and published a reconstruction. Into an examination of Abel's conclusions I will go more fully at a later stage.

(f) G. M. Allen investigated in 1921 a fragmentary skull of some considerable importance from an unknown locality in the United States, which he assigned to a new genus *Archaeodelphis*. In discussing the affinities of the skull he referred to *Prosqualodon*, which he grouped with such primitive genera as *Agorophius* and *Patriocetus*, basing his conclusions on Abel's previously published work.

(g) In 1923, Kellogg published an important work in which he revised the whole classification of the shark-toothed cetaceans. Again following out Abel's suggestions, this author was compelled to attribute to *Prosqualodon* a more primitive place in the cetacean series than it deserves.

(h) The phylogeny of the Cetacea was discussed by Dart in 1923 as the result of an examination of the brain casts of certain zeuglodonts and of *Prosqualodon*. He came to the conclusion that *Prosqualodon* is near the stem-line of modern Cetacea but that none of the zeuglodonts at present known could be regarded as ancestral to living whales.

(i) G. S. Miller (1923) suggested that, if the parietals formed a broad band across the vertex as described by Abel, this character would place the genus *Prosqualodon* in a family of its own.

(j) In a most important communication made in 1926, Cabrera was able to add fundamentally to our knowledge of the type skull of *Prosqualodon australis*, and with the help of further material he threw new light on the question of the dentition in this form. He did useful service in correcting inaccuracies in previous descriptions.

(k) The accession of the new information made available by Cabrera enabled Kellogg to assign a more reasonable position to this genus in the classification of the group, which he did in his "History of Whales" (1928). Here *Prosqualodon* was given rank with *Squalodon* and other genera in a single family, the Squalodontidae.

(l) Recently Frenguelli (1928) has recorded the discovery, in the Chubut beds, of a mutilated left humerus presumably belonging to *Prosqualodon australis*. This humerus bears marks which have been attributed to human agency.

(m) Flynn, in a preliminary communication (1932), gave a short diagnosis of *Prosqualodon davidi*, a new species, from the Miocene Beds, Table Cape, Tasmania.

(n) In 1936 appeared Slijper's outstanding monograph, "Die Cetaceen, vergleichend—anatomisch und systematisch", in which many references are made to *Prosqualodon*, above all, in an important section (Kap. 19) dealing with the Phylogeny of the Cetacea.

(o) In 1937, Benham announced the discovery of a very complete skull with associated teeth, an atlas, an axis and two other cervical vertebrae and a scapula, all found in the Caversham Quarry, Dunedin, New Zealand, in strata referred to Upper Oligocene and forming the type of a new species *Prosqualodon hamiltoni*. Some other vertebrae, a mid-lumbar and a group of seven caudal, found at Milburn, N. Z., in what are regarded as Upper Oligocene Measures, were also referred to the same genus and species.

## II. DESCRIPTION OF *PROSQUALODON DAVIDI*.

### (a) DISCOVERY, LOCALITY, ETC.

The remains of this fossil were discovered by myself in September, 1919, at Wynyard, Tasmania, and preliminary notes announcing the find have already appeared (Flynn, 1920, 1932). The beds in which the remains were found are regarded as being of miocene age\* and form part of the well-known headland, Table Cape, Tasmania. This forms a conspicuous "bluff" just outside the town of Wynyard, N.W. Tasmania. Between the township and the cape the River Inglis empties into Bass Strait. The bluff directly overlooks the open ocean and its base is washed by the waves at high water. Naturally a considerable amount of "weathering" goes on. Large boulders which, from time to time, have broken away, line the base of the cliff. It was a recent breakaway of this type that accounted for the exposure of the remains of *Prosqualodon davidi*.

Portion of the fossil was showing in the face of the cliff some twenty-five feet above the base and from this position were taken a number of thoracic, lumbar and caudal vertebrae, the sternum, the right tympanic and a molar tooth. From a fallen block below were obtained the skull and right ramus of the mandible, a number of teeth of the left ramus and the scapula and humerus of the right side, while the left paddle was represented by the radius, ulna, carpals and meta-carpals, all in position.

Comparison of the loose tympanic with that attached to the skull and of the molar tooth found in the cliff with those of the skull show without doubt that all the remains belong to a single individual.

\* Hall (1911, p. 263) was inclined to regard these beds as being of eocene age but his opinion is not supported by others.



As originally found, the right mandibular ramus was almost in its natural position with regard to the skull. The tip of the mandible is missing. Of the left ramus nothing remained; almost all its teeth were recovered, however, and curiously enough were all in their natural position. It would appear as if the mandible had rotted away from the teeth without disturbing them.

The skull is in a magnificent state of preservation. It is without question the best preserved skull of this type of whale yet discovered. There are no very bad fractures and there is an entire absence of distortion. All the teeth of the upper jaw are preserved *in situ*, many of them absolutely intact.

The original fossil is now in the Department of Biology, University of Tasmania, but casts of the skull and mandible have been placed in the Museum of Natural History, London, in the Department of Zoology and Comparative Anatomy, University College, London, in the American Museum of Natural History and in other institutions.

I have already published (1932) a short diagnosis of this new species which I have had great pleasure in naming after the late Professor Sir T. W. Edgeworth David, K.C.B., C.M.G., D.S.O., B.A., D.Sc., F.R.S., of the University of Sydney, eminent in Australasia in the fields of geological teaching and research.

(b) SKULL CHARACTERS. (Pl. I, figs. 1-3; Pl. II, fig. 13.)

The skull is in general quite of the cetacean (squalodont) type and has a total length of 54.8 centimetres. The rostrum is about half the total length of the skull. Looked at from above, the rostrum has the form of a triangle with somewhat concave sides. Viewed laterally, it is seen to be gently concave on the upper surface, so that the end of the snout is slightly elevated. The nasal openings are not so far back as in *Squalodon*. The nasal bones roof the posterior portion of the external nasal chamber. The maxillae almost cover the supra-orbital processes of the frontals. Each supra-orbital plate of the frontal is strongly developed, especially as regards its exposed edge. The zygomatic process of the squamosal is very powerfully developed. The temporal fossa is of medium depth. The supra-occipital is large and shield-shaped, extending upwards and forwards to meet the frontals, thus preventing the parietals from entering into the formation of the cranial roof. The dorsal surface of the vomer bears an exceptionally wide, open groove for the reception of the cartilaginous portion of the mesethmoid. The palatines are well developed, meeting in the midline and extending back between the pterygoids. The latter form a part of the posterior surface of the bony palate. Each ends postero-ventrally in a well-developed hamular process. The periotic and tympanic bones are typically cetacean. The mastoid is fully exposed on the ventral side in a wide, open groove between the paroccipital process and the post-glenoid process of the squamosal. The jugal is very slender, much more so, for example, than is the case in *Squalodon bariense*. Ethmo-turbinal bones are fairly well developed.

*Skull foramina.*—A pair of large olfactory foramina are present in the cribriform plate. The optic foramen, the sphenorbital foramen (foramen lacerum anterius) and the foramen rotundum open into a common sinus externally but are separated by well-developed bony walls internally. The foramen ovale and the foramen

lacerum medius are confluent. The basi-sphenoid is perforated on each side by the *carotid foramen* for the transmission of the internal carotid artery. The ascending plate of the palatine is notched by a large spheno-palatine (orbito-nasal) foramen.

*Mandible.* (Pl. II, figs. 8 & 9).—The coronoid process is low. The symphysis is of medium length, extending back to the level of the anterior molar. The condyle is small, projecting strongly externally.

*Dentition.*                      I.  $\frac{3}{3}$ .    C.  $\frac{1}{1}$ .    PM.  $\frac{4}{4}$ .    M.  $\frac{6}{6}$ .

*Molars.* (Pls. III & IV).—All molars are two-rooted, with roots connected by an isthmus, which is possibly a vestige of an original third root. The two posterior molars in the upper jaw and the posterior one of the lower jaw are relatively much smaller than the others. The molars are closely set in the jaw, slightly overlapping in some cases. The arrangement of the edge cusps of the molar teeth is of the type in which there are three anterior and three posterior cusps making, with the main cusp, seven in all.

*Premolars.*—These have the roots coalesced but separated by a groove, almost obliterated in the case of the anterior premolars.

In all teeth the enamel is extremely rugose, the whole surface except the extreme tips of the cusps being covered with nearly parallel ridges, often beset with minute sharp denticles.

In general the skull is very rounded, much more so than is the case in *Squalodon*, approaching the modern odontocetes in this respect. The bones of the side walls of the skull are inflated, and no post-orbital constriction is present. The bony crests are suppressed, as is generally the case in modern odontocetes.

The whole skull appears in a slight degree asymmetrical, due to the greater development of the bones of the left side. The distinctness of the sutures shows that the fossil is that of a young individual.

#### (c) DETAILS OF SKULL STRUCTURE.

*Premaxillae.*—The two premaxillae in their anterior extent form the entire apex of the rostrum. Here each is somewhat swollen and bears the three well-developed incisor teeth. The alveoli of these teeth are separated by a distance of about 5 mm. The anterior alveolus is almost horizontal, facing almost directly forwards. The two succeeding alveoli on each side are inclined forward, downward and outward. Passing backward, each premaxilla in its facial aspect becomes extremely narrowed, particularly about the level of the second premolar. Posteriorly to this the bones become gradually wider and each rises by a gentle slope to end in a rounded margin at the level of the fronto-nasal suture. In this region, therefore, the premaxilla presents a large exposed surface by which it descends laterally to the maxilla.

The rostral groove is very wide. The anterior part of its floor is composed of the combined premaxillae but farther back these bones are entirely concealed by the vomer, except along a narrow dorsal strip situated on each side near the dorsal edge of the groove. This exposure increases in area posteriorly. Only

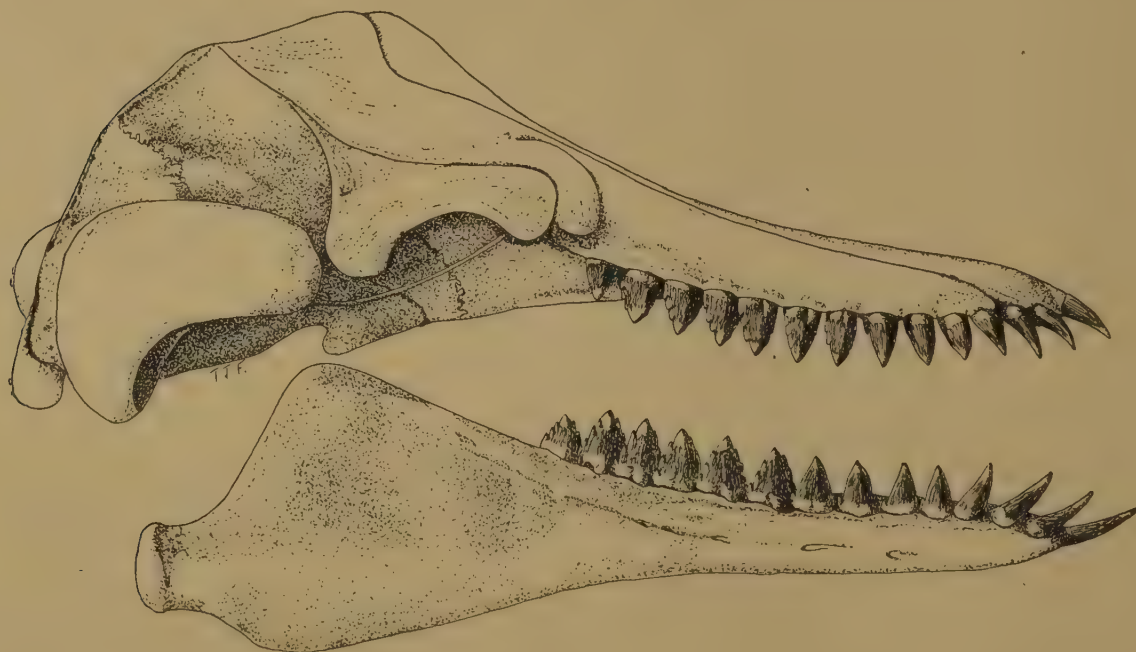


in the middle of its facial extent is there any attempt on the part of either premaxilla to roof the rostral groove and this effort is of the slightest. In this region the facial surface of each bone bears a large blood foramen. Just here, also, the right premaxilla is depressed below the left, is slightly wider and has a sharper admesial border. This difference corresponds with a slight shift of the posterior part of the rostral groove to the left.

In their palatal exposure the two premaxillae together form a long triangular area wedged in between the anterior ends of the palatine plates of the maxillae. At their posterior ends on this surface they together meet the vomer, the keel of which is here exposed to a slight extent between the two maxillae.

*Maxillae.*—In their facial portions the shape of these bones determines almost wholly the rostral contour. In view of the fact that, in previously described

Text-figure 1.



Skull and lower jaw of *Prosqualodon davidi*, viewed from the right side. The lower jaw has been reconstructed as far as the apex is concerned. ( $\times \frac{2}{7}$  app.).

specimens of this genus, the end of the rostrum is missing, it is of some importance to determine where fracture is likely to occur in order that in those specimens accurate restorations of this region of the upper jaw may be possible.

Looked at from above, each maxilla is concave externally. The external border curves inward as it passes forward from the antorbital notch, maintaining this trend until it reaches the level of the second or third premolar, when the curve flattens out to meet the edge of the premaxilla. The result of this is that the rostrum is of least diameter about the level of the second premolar and it is in this region that the rostrum is weakest and that fracture is most likely to occur.

The posterior portion of the maxilla consists of a wide expansion which, together with the underlying extension of the frontal, forms the supra-orbital plate. The maxillary plate does not entirely cover that of the frontal, a fair proportion of

the latter being exposed at the margin. There is some lack of symmetry here, the frontal being more covered on the left side than on the right.

External to the antorbital notch is formed the antorbital process of the maxilla, which is produced downwards in the manner of a scroll over the anterior edge of the frontal apophysis. The antorbital notch of the left side is somewhat deeper and wider than that of the right.

Postero-mesially, on the dorsal side, the maxillary plate meets the anterior border of the supra-occipital for a short distance laterally to the body of the frontals. In front of this the maxillary plate is fairly deeply concave, so that it rises by a rather steep face to meet the lateral edge of the median frontal plate.

The maxillae form the greater part of the hard palate, the posterior portion of which is completed by the palatines and pterygoids. The bony palate is strongly convex from side to side in its maxillary and palatine regions, thus contrasting greatly with the tendency to contraction in this region in modern odontocetes. Along the alveolar border of the maxilla are set the maxillary teeth consisting of the canine, four premolars and six molars on each side.

About the middle of the palatal surface of each maxilla there is a distinct foramen from which a groove passes forward. This is the posterior palatine foramen. There are a number of smaller foramina situated farther back. Forward of the antorbital notch, each maxilla is expanded into a marked external prominence, so that at its base the rostrum is very wide and strong. Just behind this on either side the maxilla is excavated to receive the base of the malar (see text-fig. 5.)

A conspicuous feature of this aspect of the maxilla is the large foramen piercing the upright orbital plate of the bone and serving to transmit the second branch of the fifth nerve (infra-orbital foramen). The exit for the fibres of this nerve is represented by two or three apertures on each side on the facial aspect of the bone.

*Nasals.*—These are extremely interesting in that they represent a condition intermediate between the plate-like nasals of such genera as *Prozeuglodon*, *Agorophius*, *Archaeodelphis*, *Patriocetus*, etc., and the nodular form of the same bones found in modern odontocetes. Each nasal in vertical section is roughly triangular (text-fig. 4) and is about as deep as it is long. Looked at from the dorsal side each nasal is of oval form. From its lateral articulation with the premaxilla each bone passes forward and inward to meet its fellow in the midline. Together they form a definite roof to the posterior portion of the common nasal chamber. In this respect this genus shows a condition which is more primitive than that obtaining in *Squalodon*.

*Frontals.*—The exposed portion of the united frontals forms a roughly rhomboidal area on the upper surface of the braincase. The sagittal suture is indistinct but the crest is evident in the form of a low rounded elevation. The exposed portion lateral to the ridge is slightly concave. The anterior edge of each frontal is hollowed out to receive the corresponding nasal. Projecting forward for some distance between the nasals is a short median wedge-shaped process of the frontals. Posteriorly, in their central portions, the frontals come into direct contact with the anterior border of the supra-occipital, in this way preventing the parietals from appearing in the roof of the cranial cavity. Laterally, each frontal dips



somewhat suddenly downwards into the large and expansive supra-orbital plate of the frontal, which terminates externally in the extremely thick and curved ledge which forms the external and upper border of the orbit. There are ant-orbital and post-orbital processes, over the former of which is curved in a vertical direction the corresponding scroll of the maxilla. As previously pointed out, there is a slight difference in the amount of overgrowth of the maxillary plate, there being more of the frontal exposed on the right side than on the left.

*Parietals*.—Each of these has the usual form of a hollow lamina constituting the greater part of the side wall and floor and some of the roof of the temporal fossa. The parietals take no part whatever in the formation of the roof of the braincase. They are prevented from meeting in the midline above by the extension forward of the supra-occipital to meet the frontals. In front of each parietal a limited portion of the alisphenoid enters into the floor of the temporal fossa.

The occipito-parietal suture forming, as it does, the lateral descending portion of the lambdoidal suture, is borne on a prominent crest, not nearly so elevated, however, as it is in *Squalodon*, nor does it form a projecting shelf or plate as in *P. hamiltoni*. As it descends, the crest becomes very low and rounded, but it is still possible to detect, although with difficulty, the division of the crest into two, one branch passing towards the squamosal, the other towards the occipital region. This arrangement recalls the conditions in this region as found in *Prozeuglodon* (Andrews, 1906, p. 246.)

The parietals in general are more inflated than they are in the Archaeoceti. This is to be associated with the early and pronounced basal expansion of the brain (Dart, 1923), a phenomenon which, in conjunction with telescoping (G. S. Miller, 1923), prevents any possibility of the parietals extending upwards to meet at the vertex of the braincase.

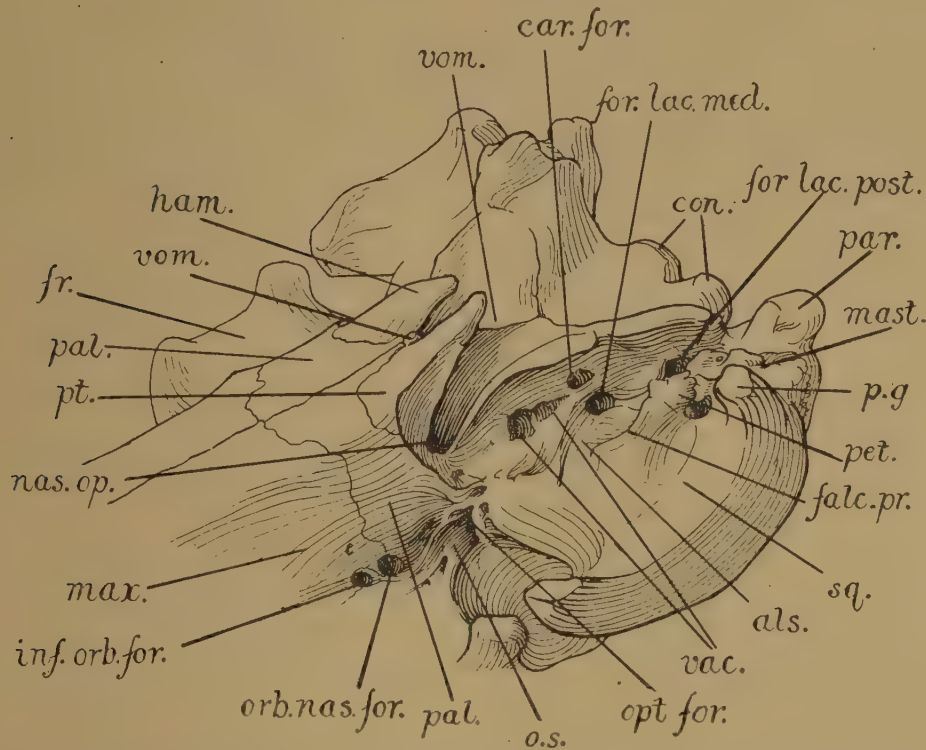
*Supra-occipital*.—This is tremendously developed, being a large shield-shaped bone which, from its union with the exoccipital below, extends upwards, curving forwards to meet, in the centre above, the combined frontals. Antero-laterally, it has contact for a short distance with the backward extension of each maxilla. The remainder of each lateral margin meets the parietal and the squamosal. Below, it is united with the exoccipital but the line of suture is obliterated.

The tendency towards the rounding of the braincase has had its effect on the supra-occipital. In the Archaeoceti and in *Squalodon*, the bone becomes greatly excavated for muscle attachment; in *Zeuglodon osiris* this hollowing out is at its maximum. The lambdoidal crest in these therefore becomes particularly prominent. *Prosqualodon*, however, foreshadows in this region the arrangement found in modern odontocetes. In these the great expansion of the brain and the loss of muscle development, associated with a diminishing mobility of the neck, have caused the supra-occipital to become convex instead of concave. In *P. hamiltoni*, however, it is said to be concave.

*Basi-occipital*.—The suture between this bone and the basi-sphenoid is entirely obliterated. On the ventral side the basi-occipital is seen to form a wide shallow gutter limited laterally by the prominent wings which are characteristic of the bone in this region. They extend downwards and outwards and become continuous in front with the similar wings of the pterygoids.

These processes were but little developed in the *Archaeoceti* (Stromer, 1903, tafel v (ii), fig. 1). Posteriorly, the basi-occipital contributes to the formation of the inner lower portion of each condyle and extends across between the two condyles as a prominent bridge. It also helps to form the inner boundary of the foramen lacerum medius.

Text-figure 2.



View of the right side of the skull. It is shown ventral side uppermost but tilted slightly towards the observer so that the foramina of the right side can be seen. (Drawing by Miss Joyce Townend.)

als.=alisphenoid; car.for.=carotid foramen; con.=condyle; falc.pr.=falciform process; for.lac.med.=foramen lacerum medius; for.lac.post.=foramen lacerum posterius; fr.=frontal; ham.=hamular process of the pterygoid; inf.orb.for.=infra-orbital foramen; mast.=mastoid; max.=maxilla; nas.op.=internal opening of right nasal passage; opt.for.=optic foramen; orb.nas.for.=orbito-nasal foramen; o.s.=orbito-sphenoid; pal.=palatine; par.=paroccipital process; pet.=petrosal; p.g.=post-glenoid process of the squamosal; pt.=pterygoid; sq.=squamosal; vac.=vacuities in the skull floor; vom.=vomere.

*Squamosals*.—These have the usual relations but each bone in *Prosqualodon davidi* is large and powerful. The zygomatic process is a relatively tremendous structure, much larger in proportion than it is in *Squalodon*. It is particularly well developed in its post-glenoid portion. As already pointed out, the ventral portion of the lambdoidal crest which, in *Prozeuglodon* runs down “in an S-shaped curve, then being continuous with the sharp upper border of the zygomatic process” (Andrews, 1906, p. 248), is in *Prosqualodon davidi* as it is in *P. australis*, just recognizable as being continuous with a low rounded elevation on the dorsal

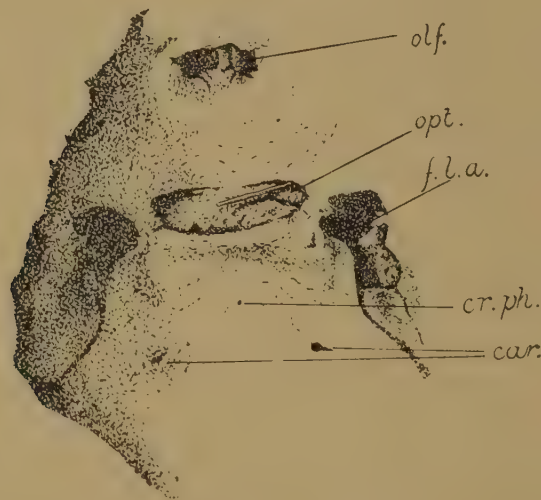


side of the zygomatic process of the squamosal. In the tremendous strength of the zygomatic process, with its smooth external contours and solid cross-section, the squalodonts are very specialized.

The falciform process is low. There is a fairly considerable exposure of the squamosal within the cranial cavity. Between the prominent posterior end of the post-glenoidal process and the paroccipital process is a wide and deep groove in which the mastoid is fully exposed. The mastoid is closely united with the post-glenoid process.

*Exoccipitals*.—These bones have the usual arrangement. Laterally, each is produced downward into the very large, prominent, rounded paroccipital process between which and the post-glenoid process of the squamosal lies the deep groove in which the mastoid is exposed. The exoccipital on each side forms the posterior boundary of the large foramen lacerum posterius. The occipital condyles are

Text-figure 3.



View of the interior of the cranial cavity through a break in the back of the skull. *car.*=internal openings of the carotid foramina; *cr.ph.*=internal opening of the cranio-pharyngeal canal; *f.l.a.*=foramen lacerum anterius; *olf.*=septum between the olfactory foramina; *opt.*=optic groove showing a seeker passing into the right optic foramen.

extremely well developed, supported each on a distinct pedicel, and are markedly convex. Each measures 58 mm. greatest length by 25 mm. greatest breadth. In the fact that the condyles are raised on distinct pedicels and are consequently very prominent, *Prosqualodon davidi*, *P. australis* and probably *P. hamiltoni* are very different from most modern odontocetes. In this respect *Squalodon*, in some of its species (e. g. *S. calvertensis* Kellogg), seems to be less primitive than *Prosqualodon*.

*Basi-sphenoid and Pre-sphenoid*.—The limits of these bones cannot be definitely determined, since they are to a great extent covered ventrally by the posterior extension of the vomer. Laterally the basi-sphenoid is perforated on each side by the foramen for the internal carotid. This lies below the anterior end of the foramen lacerum medium. The carotid foramen leads to a canal which passes inwards, forwards and upwards to open on the floor of the cranial cavity, one

on each side (text-fig. 3, *car.*). The two foramina are situated one at each end of a shallow transverse depression which represents the pituitary fossa. These carotid foramina are also to be seen opening on the floor of the cranial cavity in the skull of *P. australis* in the British Museum.

Somewhat in advance of these, on the cranial floor, there is to be seen in the midline in *P. davidi* a small but quite distinct foramen in the pre-sphenoid leading to a canal which pierces the cranial floor (text-fig. 3, *cr.ph.*). The external opening is hidden by the posterior extension of the vomer. This canal, which, it is stated, lodges a vestige of the notochord, is found in insectivores and in some other mammals (Gregory, 1910, p. 245) and is also present in the young of living whales (Ridewood, 1922, fig. 4, p. 223, indicated but not lettered; De Burlet, 1913, text-fig. 19; 1915, taf. 1 & 2.)

*The vomer.*—This forms in its anterior extent a groove of relatively great width open above and running almost the length of the rostrum. The two sides of the vomerine groove increase in height posteriorly, then curve round the inner side of each blow-hole to become applied to each lateral face of the mesethmoid. The anterior and dorsal portion of the rostral groove is bounded by the premaxillae.

A small part of the vomer appears in the palate between the anterior ends of the maxillae. In its postero-ventral portion the vomer is continued backwards as a curved lamina, concave ventrally from side to side, and provided with a median keel. With this keel at its lower posterior end the palatines come into relationship.

A small recurved portion of the vomerine keel appears at the end of the hard palate behind the conjoined palatines and between the hamular processes of the pterygoids. Behind this the keel quickly decreases in height and soon fades away. The vomer, therefore, in its posterior extent takes the form of a curved plate which underlies the basi-cranial axis. This backward extension hides from view the pre-sphenoid and part of the basi-sphenoid. It is not, however, in close contact with the skull base, there being quite a well-marked space between the vomerine plate and the overlying sphenoidal bones. The plate ends behind in a prominent curved transverse ledge. This arrangement is the precursor of that of modern toothed whales in which the backward extension of the vomer is an extremely thin plate whose close approximation to the base of the skull amounts practically to a fusion.

Laterally, in this region, the vomer articulates with the large pterygoid wings.

*Ali-sphenoids.*—On each side the ali-sphenoid lies between the squamosal externally and the basi-sphenoid internally. Posteriorly it comes into relation with the exoccipital while it meets anteriorly and internally the pterygoid.

Along the anterior boundary it comes into contact with the parietal also for a space and here, to a limited extent, it forms a part of the anterior floor of the temporal fossa. A forward extension of the bone curves under the large common opening of the optic and sphenorbital foramina, comes into contact with the pterygoid ventrally (pterygoid process of the ali-sphenoid) and here takes the form of a small vertical plate. The internal line of demarcation of the ali-sphenoid against the pterygoid and basi-sphenoid is extremely open and there is a number of irregular spaces and channels in this region.



The large oval foramen lacerum anterius (sphenorbital foramen), from the posterior margin of which passes back the wide and shallow groove for the trigeminus, is very obvious within the skull (text-fig. 3, *f.l.a.*). The skull wall is extremely thick, so that all the foramina in the side wall lead to tolerably long canals. Below the sphenorbital canal and passing outwards from the trigeminal groove to open into the sphenorbital canal before its exit, is the foramen rotundum. The foramen lacerum anterius, the foramen rotundum and the optic foramen all open into one space or arcade situated in the orbit. In its posterior extent the alisphenoid forms the anterior and most of the external boundary of the foramen lacerum medius with which the foramen ovale is confluent.

*Orbito-sphenoids.*—As exposed in the orbit each of these bones appears as a moderately narrow band extending diagonally outwards, bounded in front and behind by the frontal. The anterior and posterior limits of the orbitosphenoid

Text-figure 4.

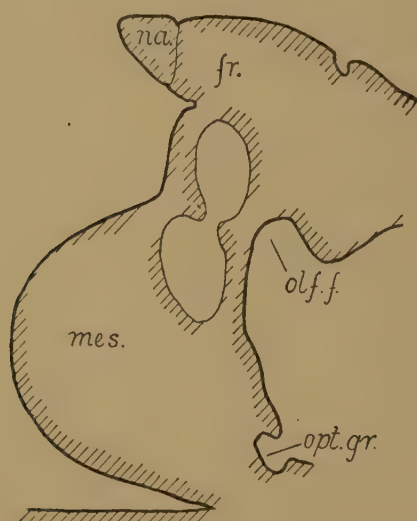


Diagram of a sagittal section through the olfactory region of the skull. *fr.*=frontal; *mes.*=mesethmoid; *na.*=nasal; *olf.f.*=olfactory fossa of the cranial cavity; *opt.gr.*=optic groove for the accommodation of the chiasma.

are indicated by distinct ridges on which the sutures are borne. Consequently, the bone, from below, has the look of a wide shallow furrow which leads into the common space or arcade into which open the optic and sphenorbital foramina together with the foramen rotundum. Within the cranial cavity can be seen the deep groove in which is lodged the optic chiasma (text-fig. 3, *opt.*). From each end of this the canal for the transmission of the optic nerve arises and passes forwards and outwards to open into the external chamber mentioned above. The extent of solid bony wall separating this canal and that of the foramen lacerum anterius can be seen within the braincase. The two canals, however, are confluent for about half the thickness of the skull. It is into this common canal that the foramen rotundum opens.

*Mesethmoid.*—The posterior end of the rostral groove is occupied by a vertical

plate which represents the lamina perpendicularis of the mesethmoid. In its lower portion this is closely embraced by the vomer and it is here a somewhat swollen bone which projects forward a little into the rostral groove. Above, it narrows, quickly running backwards and upwards to broaden out into a curved plate supporting the frontals and nasals. The lamina perpendicularis becomes continuous posteriorly with the cribriform plate which closes the cranial cavity anteriorly. The olfactory foramina are represented by two large openings, one on each side of the plate, these leading each to a canal, of fair width, which passes upwards and forwards to open into the single large space into which the blow-holes open. Text-fig. 4, *p.* represents a vertical longitudinal section of this region. It will be seen that there is a distinct olfactory fossa in the cranial cavity and further it should be noted that the mesethmoidal partition between the olfactory canals is not complete. The whole arrangement recalls strikingly the condition of the olfactory apparatus found in the Archaeoceti (Elliot Smith, 1903; Dart, 1923). The interest of this region is increased, if anything, by the occurrence of well-developed ethmo-turbinals. Each of these consists of a bony knob of spongy texture and of somewhat complex form, having the surface marked by shallow grooves. Each ethmo-turbinal is set by a broad lateral face on the corresponding maxilla and is united above with the expanded mesethmoid. While the arrangement does not point to the highest development of the olfactory sense, it certainly suggests a condition considerably more primitive than the almost complete anosmatism of living odontocetes.

*Lacrymals.*—The lacrymal is present as a small area on the ventral aspect of the anterior margin of the orbit, where it lies between the frontal and the maxilla, with which bones it is thoroughly fused. It has no apparent contact with the jugal (text-fig. 5).

In *Prozeuglodon atrox* (Andrews, 1906, p. 248) the lacrymal is a small element forming a slight projection at the anterior border of the orbit and wedged in between the frontal, the jugal and the maxilla. The position of the lacrymal of *Prosqualodon davidi* is arrived at by (*a*) antero-lateral extension of the supra-orbital plate of the frontal, resulting in the position of the lacrymal becoming more internal, (*b*) the extension of the maxilla into its supra-orbital apophysis and the development of the antorbital scroll, with the result that the lacrymal becomes entirely covered from the dorsal side.

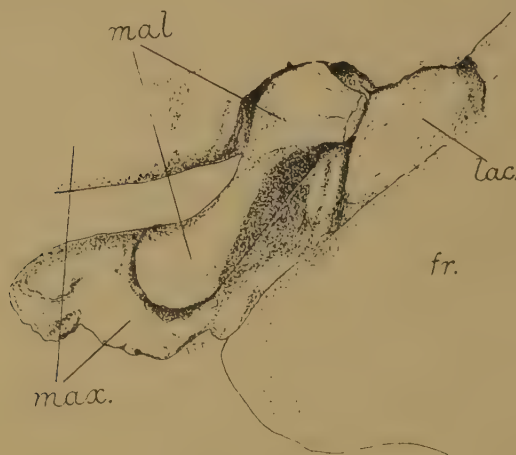
The position here assigned to the lacrymal seems to be more reasonable than that suggested for the same bone in *Squalodon calvertensis* (Kellogg, 1923, p. 51; see his remarks on the position of the lacrymal in the Iniidae, p. 51; Gregory, 1920, p. 159, text-fig. 102, showing the position of the lacrymal bone in a young *Mesoplodon grayi*).

*Jugal.*—The anterior end of this bone is sunk into a pit in the posterior end of the alveolar border of the maxilla just in front of the lacrymal (text-fig. 5). The base of the bone in this position curves outwards in a curious way on to the antorbital scroll of the maxilla but does not come into contact with the frontal. The remainder of the bone is an extremely slender rod, flattened from above down, broken off as indicated in text-fig. 5. Its posterior area of attachment is indicated by a slightly concave facet on the ventral side of the zygomatic process of the squamosal at its anterior end.



*Palatines.*—The palatines occupy the posterior portion of the hard palate meeting in the midline. Each gives rise to a median backward extension. These two together preventing the two pterygoids from meeting. The combined backward extension is tipped by the end of the ventral portion of the vomerine keel. Anteriorly the palatines are separated from the maxillae by well-marked transversely disposed sutures; behind, each is shaped to receive the curved anterior face of the corresponding pterygoid. Within the blow-hole the palatine forms a fair proportion of the antero-lateral aspect. The orbital plate of each palatine passes upwards and backwards as a continuation of the orbital plate of the maxilla. This plate is notched by the very large spheno-palatine (orbito-nasal) foramen for the transmission of the second branch of the fifth cranial nerve. This foramen passes directly upwards and backwards to open into the blow-hole. It is, as is well known, quite insignificant in modern odontocetes. Postero-laterally the

Text-figure 5.



Ventral view of part of right side of skull to show the relations of the molar and lacrymal.

*fr.*=frontal; *lac.*=lacrymal; *mal.*=malar; *max.*=maxilla.

orbital portion of the palatine forms part of the external wall of the post-palatine sinus. The remainder of this wall is formed by the external wall of the pterygoid duplication.

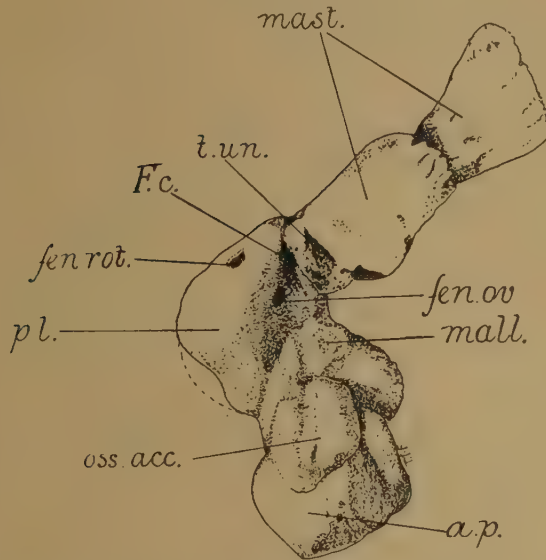
*Pterygoids.*—These bones enter into the formation of the posterior end of the hard palate and still farther back form on each side a double plate which encloses the so-called post-palatine sinus. The palatine portion of each pterygoid is produced backward into a conspicuous hamular process. The pterygoids are prevented from meeting in the midline by the median prolongation backward of the two palatines. From here the suture line with each palatine curves transversely across the palatal surface and then extends posteriorly till it reaches the rim of the external wall of the post-palatine sinus. A good deal of the outer wall of this sinus is therefore composed of palatine.

It is instructive to compare the conditions obtaining in this region of *Pro-squalodon* with those to be found in the skull of Archaeoceti. A discussion of the results of such a comparison will be found later in this paper. The mesial

wall of the pterygoid is in *Prosqualodon davidi* a vertical plate which curves outward round the blow-hole and continues backward on each side to form the ventral wing which lies laterally to the vomer and forms on each side the boundary of the wide and fairly deep mesopterygoid fossa. Posteriorly these wings are directly continuous with the similar processes of the basi-occipital.

*The periotics.*—Both these have been preserved. The tympanic of the left side was broken away in the manipulations connected with casting and was cemented back wrongly by the operator, so that it cannot be moved again without risk. The other tympanic is loose. The right petrosal is therefore freely visible from the inferior (tympanic) aspect.

Text-figure 6.



Petrosal bone of the right side, ventral view.  
*a.p.*=anterior process; *F.c.*=Fallopian canal;  
*fen.ov.*=fenestra ovale; *fen.rot.*=fenestra  
 rotunda; *mall.*=depression for head of  
 malleus; *oss.acc.*="accessory ossicle"; *t.un.*  
 =area of union with the tympanic.

Text-figure 7.



The stapes of *Prosqualodon davidi*. (×5).

The petrosal (text-fig. 6) differs very much from that of *Patriocetus* (Abel, 1914, text-fig. 3) or of *Squalodon bellunense* (Dal Piaz, 1916, text-figs. 1 & 2). The anterior process is very much expanded and ends in a somewhat blunt point. It is divided superficially into two by a constriction. The pars labyrinthica is strongly swollen in front and gradually tapers posteriorly to end in a rounded extremity. The Fallopian canal, at first a groove, becomes converted into a canal in its posterior extent. The fenestra ovale situated in front of the beginning of this groove is here closed by the broken-off basal plate of the stapes. On the ventral surface of the pars labyrinthica is well seen the fenestra rotunda, situated postero-internally. A characteristic feature is the presence of the so-called "accessory ossicle", fused to the ventral side of the petrosal, really belonging to the tympanic (processus tubarius of the tympanic). The tympanic is quite of



the type described and figured by Dal Piaz as occurring in *Squalodon bellunense* (1916, p. 58, figs. 3 & 4, tav.viii. figs. 6, 7, 8 and 9).

The mastoid is attached to the petrosal. It is quite visible from the lower aspect of the skull. It is intimately fused to the post-glenoid process of the squamosal but is not attached to the paroccipital process. The mastoid, as visible, consists of two parts, as shown in the accompanying text-figure. The innermost of these seems to be associated with the tympanic rather than with the petrosal. The arrangement recalls Flower's suggestion as to the double origin of the mastoid (Van Kampen, 1905, p. 647).

The remainder of the stapes was found in the matrix in this region of the skull and is reproduced in text-fig. 6. It will be seen that it presents a well-marked intercrural space.

Skull Measurements of *Prosqualodon* (in mm.).

	<i>P. australis</i>		<i>P. davidi</i>	<i>P. hamiltoni</i>
	La Plata Mus.	Brit. Mus.	Tas. Univ. Mus.	Otago Univ. Mus.
Greatest length of skull .....			548	550+
Length of rostrum .....			270	24+
Length, occipital condyle to base of rostrum .....	330	285	255	
Length of posterior seven alveoli of upper jaw .....		130	145	
Length from occipital condyle to posterior alveolus .....		311	282	
Bizygomatic diameter .....	450 (?)	336	330	340
Greatest width between margins of supra-orbital plates .....	426	316	314	280 (?)
Least width between orbits .....		96	99	
Width of base of rostrum at ant-orbital notch .....	240	188	188	
Outside width of rostrum at middle of posterior alveolus .....	228	187	191	
Outside width at middle of fifth alveolus from posterior end ....		122	109	
Outside width at middle of seventh alveolus from posterior end ....		83	83	

*Mandible.* (Pl. II, figs. 8 & 9.)—This is practically complete, only a few centimetres being absent from the anterior end. The condyle is complete, the coronoid is slightly broken and the angle a little chipped. Of the teeth, the three incisors, the canine and the first premolar are missing from the jaw, although the alveoli of the latter two are present. The second premolar has lost a fair amount of its crown. The remainder of the teeth are complete. The last molar is missing from the jaw but is available for examination.

The symphysis of the mandible is of moderate length, extending back to the level of the first molar. The mandible has the same twisted shape described by Lydekker for *Prosqualodon australis*.

From the condyle forwards as far as the last molar but one, the ramus is fairly straight. In front of this, however, it begins to curve outwards, the outward curvature being accompanied by a twist of such a type that the anterior teeth, instead of standing vertically in the jaw, emerge more and more laterally. Thus the long axis of the first premolar is about 45 degrees away from the vertical. In the neighbourhood of the symphysis the ramus straightens but the vertical twist is still present. The condyle measures 45 mm. by 28 mm., having the same proportions as those recorded by True (1920) for *P. australis*. As in this latter species, too, it projects strongly externally.

Measurements of the Mandible in *Prosqualodon* (in mm.).

	<i>P. australis</i>			<i>P. davidi</i>
	La Plata Mus.	Princeton Mus.	Brit. Mus.	Tas. Univ. Mus.
Total length of posterior portion containing five posterior alveoli..	420	445	305	310
Distance from condyle to posterior alveolus. ....	297	290		202
Height of jaw at coronoid process .		217		180
Distance from highest part of coronoid process to inferior margin of condyle. ....	225	204		155
Depth of jaw at posterior alveolus..	78	95		75
Length of posterior four alveoli together. ....	120	124	75	92
Length of penultimate tooth at alveolus. ....	30	30	15	21
Width of penultimate tooth at alveolus. ....		18	9	12
Length of seven posterior alveoli..	210		135	152

(d) DENTITION.

It has been maintained by Dal Piaz and others that, in *Squalodon*, any division into premolars and molars is purely arbitrary and that all teeth merge into one another as regards their general characteristics in such a way that it is very difficult if not impossible to assign to any particular isolated tooth its definite position in the dental series. For example, he instances that it is not possible in general to distinguish between the canine and the first premolar or between the last premolar and the first molar. However this may be with *Squalodon*, the difficulties are not so great in the case of *Prosqualodon* and, as will be seen



later, the teeth arrange themselves very well into sets which fit in very exactly with the notation suggested by Van Beneden.

$$\text{Dental formula.} \quad \text{I. } \frac{3}{3} \quad \text{C. } \frac{1}{1} \quad \text{PM. } \frac{4}{4} \quad \text{M. } \frac{6}{6} \quad (\text{N.V.B.}).$$

#### UPPER DENTITION.

As there are no isolated teeth of the upper dentition available, any description of these teeth can only apply to their exposed portions. As far back as the second molar the teeth are separated by definite interspaces. Behind this they are closely approximated and even overlap slightly.

*Incisors.*—These are sharp-pointed, recurved, fang-like teeth, practically circular in section at the base. Their ornament consists of low, wavy, subparallel ridges extending from the base to near the apex. Each tooth bears on its anterior and posterior face a faint median keel. In the posterior incisors this keel becomes microscopically serrated. The anterior incisor on each side is inclined almost directly forward, while the posterior two approach progressively more to the vertical.

*Canine.*—This is very similar in shape and ornament to the posterior incisor. It bears on its anterior and posterior surfaces a keel similar to that on each incisor, minutely toothed in the same way, but having the denticles of the posterior ridge appreciably larger than those of the anterior. The canines have long curved roots which perforate the maxilla, so that the tubular extremity of the root with its open pulp cavity is quite visible in the skeleton on the dorsal aspect of the maxilla.

*Premolars.*—The most anterior premolar is very like the canine but posteriorly these teeth become very molar-like as regards the crown. They become progressively more upright and more compressed as we pass backwards. The fourth premolar is a well-compressed tooth of lanceolate shape with a well-defined ridge on its anterior and posterior edges. Its ornament is similar to that of the canine bearing as it does subparallel ridges over the whole of its internal and external surfaces, except at the tip of the tooth, which is quite smooth. There are two low tubercles on the anterior edge and a pair of better developed cusps on the posterior border. The antero-posterior axes of the premolars are parallel to the long axis of the jaw.

*Molars.*—These differ from the premolars in the following respects:—

- (a) They are more compressed.
- (b) The anterior and posterior cusps or tubercles are three in number on each edge and are well developed. They are more strongly developed on the posterior edge.
- (c) The teeth are set closer together and the antero-posterior axis of each is so inclined to the axis of the jaw that the anterior edge faces somewhat inwards.

The first molar is separated from the second by a definite diastema. The remaining molars are more or less crowded together. The maximum development is attained by the fourth molar. This is a high compressed tooth with the ornamentation well marked. On each edge it bears three well-developed accessory cusps. With the exception of the tip of the crown the surface is covered with more or less parallel ridges. These ridges are raised into small denticles,

particularly well developed on the inner surface of the tooth. In general, the outline of the crown is triangular, viewed laterally, but the anterior side is slightly more curved than the posterior and the edge cusps are less developed.

The posterior two molars show signs of degeneracy, particularly the last one. Not only is this tooth smaller than those preceding it but its inclination to the jaw is such that its anterior edge faces outwards, its posterior inwards. The last molar of the right side is smaller than that of the left.

#### Upper Dentition. Measurements (in mm.).

##### INCISORS.

Anterior, height 31, diameter at alveolus, 14	
Middle, " 22, " " " 15	
Posterior, " 24, " " " 14	

##### CANINE.

Height 25, diameter at alveolus 14, length of root 31

##### PREMOLARS AND MOLARS.

	Height	Longest diameter at alveolus	Greatest transverse width
Fourth premolar ..	31	17	14
First molar .....	32	21	14
Fourth molar .....	32	25	14
Sixth molar (left) ..	22	20	13
Sixth molar (right) ..	20	20	12

*Note* :—All heights are measured on the inner side of each tooth and represent the amount of surface exposed above the alveolar edge.

#### LOWER DENTITION. (Pls. III & IV).

The whole of the dentition of the lower jaw, with the exception of two teeth, is available in a more or less complete condition. The right ramus contains the canine, four premolars (of which the second has lost its crown) and five molars, the sixth having been broken from the jaw by accident but being available for examination. All the teeth of the left side were found except two. Comparison with the right side shows that the missing teeth are the third incisor and the second premolar. All three incisors of the right ramus were recovered.

*Incisors*.—The anterior incisor is a sharp-pointed conical tooth, strongly recurved. The crown has a length of 31 mm. but is slightly incomplete. It is ornamented by irregular anastomosing ridges which are better developed on the inner face of the tooth than on the outer. The ornament is absent from the tip of the tooth. The labial side of the tooth (which is, in the natural position, ventral) presents a median ridge which passes from the base of the crown to its apex. A corresponding ridge on the lingual (=dorsal) aspect of the crown is situated somewhat externally, so that, in cross-section, the circle represented by the section is divided by these ridges into two arcs, of which the outer is the smaller. The diameter of the crown at its base is 12.5 mm. The root is almost cylindrical at the base. It possesses a large open pulp cavity. It is incomplete, so that no useful measurements can be given.



The second incisor differs in some respects from the first. It too, is a fang-like tooth, similarly ornamented to the first incisor and bearing also two minute ridges of the same type. There is slight evidence of minute serrations on these ridges in the first and second incisors. Already, however, there is to be noticed an indication of the lateral compression shown in the more posterior members of the series. The tooth is strongly recurved and, in addition, the crown is slightly bent inwards at the apex, so that the lingual side is in the smallest degree concave. The tip of the tooth is missing but the greatest length of the crown was probably some 25 mm. The crown diameter at the base is  $11.5 \times 10.5$  mm. The root is incomplete.

In accordance with the shape of the crown the root is slightly compressed at its coronal end but is more cylindrical towards the apex.

The third incisor is similar to the second. Its crown length is 23.5 mm.

#### CANINE.

Crown, length .....	22.0 mm.
„ diameter, antero-posterior .....	14.0 mm.
„ „ transverse .....	10.5 mm.
Root, length .....	30.0 mm.
„ diameter at apex .....	$7.5 \times 6.0$ mm.

As these measurements show, the canine is a somewhat compressed tooth as regards both the crown and the root. The whole tooth is very curved, the root taking part in this curvature. The ornament is similar to that of the incisors. The anterior and posterior ridges are, however, more visibly toothed. The root develops a sudden taper towards the apex.

*Premolars.*—These are differentiated from the canine by the presence of one or more well-developed accessory cusps on the anterior and posterior edges. From the molars they are also easily distinguished by the possession of a single root, the division into two being indicated at most by grooves on the external and internal surfaces of the root.

#### FIRST PREMOLAR.

Crown, length .....	20.5 mm.
„ diameter at base :	
antero-posterior .....	14.5 mm.
transverse .....	11.0 mm.

The crown is similar in shape to that of the canine but possesses a single large accessory cusp near the base on the anterior and posterior edges (the anterior accessory cusp has been broken off).

The root is incomplete but is greatly compressed.

#### THIRD PREMOLAR.

Crown, greatest height .....	21.0 mm.
„ diameter at base :	
antero-posterior .....	17.0 mm.
transverse .....	12.0 mm.

This tooth shows a more pronounced symmetry than any of those in front. As is typical for the squalodont type of dentition, the anterior edge of the crown is more curved than the posterior. On each edge there is a single large basal accessory cusp of stronger build than is the case in the anterior premolars. The posterior of these is the larger and bears a few small but well-defined denticles. The ornament of this tooth consists of fine, more or less parallel ridges all minutely toothed. The root is incomplete but is compressed. It is single but there is a longitudinal groove on its external face. No such groove is indicated on the inside of this tooth.

## FOURTH PREMOLAR.

Total length .....	53.0 mm.
Crown, greatest height .....	26.0 mm.
„ least height .....	21.0 mm.
„ diameter, antero-posterior .....	20.0 mm.
„ „ transverse .....	13.0 mm.
Root, greatest length .....	30.0 mm.

This tooth is the most symmetrical of the whole tooth series. The crown is slightly recurved. The root is straight. The enamel ornament is similar to that of the preceding tooth but there is an indication of another accessory cusp on the anterior edge above the basal one. On the posterior border there are two well-developed accessory cusps. The lower is the larger and is denticulated. The one above this is simple. The remainder of the anterior and posterior edges are lightly tuberculated. The root is simple but, on each surface, there is a sulcus almost dividing the root into two. The cross-section of the root is, therefore, hourglass-shaped, the two pulp cavities being continuous across the midline. The outer groove is deeper and wider than the inner.

In the outer groove, about one-third the distance from the lower end, is a slight prominence corresponding to the similar ridge found in this position in the molars and which, according to True, might be regarded as the vestige of an original third root.

*Molars.*—The molars all agree in the following points:—

(a) The presence of two roots connected throughout most of their extent by an isthmus.

(b) The presence in the isthmus of a curious elevation which is possibly the remaining vestige of an ancestral third root.

(c) The possession of three well-developed accessory cusps on the anterior and posterior edges making, with the main cusp, seven cusps in all.

In general the size of the molars increases from the first to the third; the fourth, fifth and sixth being progressively smaller.

The sixth is particularly small and degenerate. There is no very apparent difference in the amount of development of the last molar on the right and left side such as is found in the upper jaw. In all molars the anterior root is longer than the posterior.



## FIRST MOLAR.

Total length .....	54.0 mm.
Crown, greatest height .....	26.0 mm.
„ least height .....	21.5 mm.
„ diameter, antero-posterior .....	22.5 mm.
„ „ transverse .....	12.5 mm.
Roots, length, anterior .....	31.0 mm.
„ „ posterior .....	30.0 mm.

The crown of the tooth is ornamented with parallel ridges which bear minute cusps, these on the inner side being more conspicuous than on the outer. The three accessory cusps on each edge are well developed and are minutely tuberculated.

The tooth is two-rooted but the roots are connected by an isthmus through a great deal of their extent. Towards the crown the roots are practically coalescent being separated only by grooves on their external and internal faces respectively. The outer groove is the better developed of the two. The isthmus is of such a length that only about one-fifth of each root is free. Its lower edge has an irregular frayed-out appearance. In the isthmus appears a small longitudinal elevation referred to above as a possible rudimentary third root. This is more prominent on the outer surface.

*Second molar.*—In all essential points of structure this tooth agrees with the first molar. The crown ornament, however, is more rugged, particularly on the inner surface. The crown is higher, the roots are longer and more of each root is free of the isthmus. The suggested vestige of the third root is somewhat better developed.

Total length .....	59.0 mm.
Crown, greatest height .....	26.0 mm.
„ least height .....	21.0 mm.
„ diameter, antero-posterior .....	22.0 mm.
„ „ transverse .....	14.0 mm.
Root, length, anterior .....	34.0 mm.
„ „ posterior .....	31.0 mm.

*Third molar.*—This is the tooth which was figured in the preliminary note as the fourth molar (Flynn, 1920). The anterior root is slightly incomplete. The edge cusps on this tooth are very large.

As usual they are better developed on the posterior edge than on the anterior. The ornamentation is similar to that of the preceding tooth. About one-third of the length of the root is free of the isthmus.

Total length .....	55.0 mm.
Crown, greatest height .....	29.0 mm.
„ least height .....	21.0 mm.
„ diameter, antero-posterior .....	24.0 mm.
„ „ transverse .....	14.0 mm.
Roots, length, anterior .....	broken.
„ „ posterior .....	28.0 mm.

*Fourth molar.*—This tooth is very similar to those in front of it. The fifth and sixth molars show obvious signs of degeneration, especially the sixth.

## SIXTH MOLAR.

Total length .....	41.5 mm.
Crown, height .....	20.0 mm.
„ diameter, antero-posterior .....	21.0 mm.
„ „ transverse .....	14.0 mm.
Roots, length, anterior .....	27.5 mm.
„ „ posterior .....	22.0 mm.

The crown is strongly recurved and has the usual number of well formed accessory cusps on the anterior and posterior borders. The lowest on the anterior side is particularly rugged, being flanked by smaller ones (text-fig. 8). The rugosity

Text-figure 8.



Posterior molar of the left ramus of the mandible; anterior view (natural size).

of the inner face of this tooth is nothing short of remarkable (Pl. II, fig. 12). The roots are slightly hooked and there is a tendency towards closure of the pulp cavity below. The isthmus involves a little more than half the length of the root. In this isthmus the suggested vestigial third root is prominent.

## (e) PECTORAL GIRDLE AND FORE-LIMB.

*Right Scapula.* (Pl. II, fig. 14).—This is beautifully preserved and is practically complete. It is quite of the broad cetacean type, consisting of an expanded plate whose supra-scapular border is convex while the coracoid and glenoid borders are concave. The prespinous fossa is much reduced in extent. The spine begins as a low ridge near the supra-scapular border and passes downwards and forwards, increasing in height, to end in the very well-developed, much flattened acromion. The spine never becomes confluent with the coracoid border but remains separated from it by a rather wide (10 mm.) but shallow depression. There is no definite coracoid process but this portion of the glenoid fossa is somewhat more prominent than the remainder.

Benham (1937, p. 12, pl. 7, fig. 14) has recently figured and described the scapula of *Prosqualodon hamiltoni*. It is much larger than that of *P. davidi*. In *P. hamiltoni*, too, the coracoid process is much better developed than in *P. davidi*, while the neck of the scapula in the former species is longer and more slender than in the latter. The result is that the distance between the lower edge of the acromion and the anterior edge of the glenoid fossa (coracoid) is appreciably greater.



## Measurements (in mm.).

	<i>P. hamiltoni</i>	<i>P. davidi</i>
Greatest width between coracoid and glenoid borders. ....	250	195
Greatest depth between supra-scapular border and glenoid fossa ....	170	132
Glenoid fossa :		
Antero-posterior diameter ....	70	57
Transverse diameter ....	45	37
Acromion :		
Length ....	125	60
Width ....	45	27
Distance, upper edge from supra-scapular border ....	70	60
Distance, lower edge from coracoid	50	18

It is worthy of note that the scapula of *Zeuglodon osiris*, as described by Stromer, if it be complete, shows signs of retrogression in the coracoid process. The scapulae of *Squalodon* and *Proberodon* (Dal Piaz, 1916, tav. ix, figs. 13 & 14; Cabrera, 1926, p. 386) are similar in general shape to that of *Prosqualodon*, both presenting reduced prespinous fossae but the coracoid process in each is better represented. Among living odontocetes, *Platanista* and *Prodelphinus* possess scapulae in which the coracoid process is absent.

*The fore-limb.* (Pl. I, figs. 5 & 6).—Of the right flipper the humerus is preserved, together with the radius and ulna. What is missing in the limb of the right side is preserved in that of the left, so that a full description can be given of the skeleton of the limb. The state of fusion of the various parts is intermediate between the condition of free movement and that found in present-day odontocetes in which the bones are firmly fixed at the elbow and wrist joints. In *Prosqualodon* the limb undoubtedly served the purpose, as it does at the present day, of a planing and guiding mechanism, but it had not been so completely converted to this function as in living whales. In *Prosqualodon* there was a very wide range of movement at the shoulder but, at the elbow, the bones are well on their way towards fusion, although in life there must have been some independent movement at this joint.

At the wrist the carpals were probably embedded in cartilage as at present. The arrangement of the whole limb skeleton bears a striking resemblance to that characteristic of present-day ziphioids.

*Right humerus.* (Pl. I, fig. 5).—The epiphysis is missing from the lower end. The epiphysis of the left humerus is preserved, attached to those of the ulna and radius. All the epiphyses of these three bones are distinct and easily recognizable. The humerus is short, flattened and curved with the convexity forward. The anterior edge is therefore convex, the posterior concave. At the upper end can be seen the large rounded head with the two tuberosities. Of these latter the greater tuberosity is to a great extent suppressed but the lesser is fairly large and is continuous with the head of the bone. A bicipital groove is recognizable as a fairly wide but quite shallow depression. In the British Museum there is a cast of the humerus of *Zeuglodon hydrarchus* (= *cetoides*).

with which the similar bone in *Prosqualodon* can be compared. It is found that, in the zeuglodont humerus, there is a comparable suppression of the greater tuberosity combined with a characteristic twist of the shaft of the bone, which is much more accentuated in *Prosqualodon davidi*.

Examination of the mounted skeleton of the present-day odontocetes will show that the adaptation of the flipper to its use as a balancing and planing apparatus requires that the flipper be held extended, laterally and downwards, with its palmar surface facing ventrally. Looking at the right humerus of *Prosqualodon davidi* it seems probable that this position is attained (a) by an anti-clockwise rotation in the glenoid cavity, made possible by the suppression of the greater tuberosity, (b) by a clockwise twist of the distal end of the shaft of the humerus. In the case of the left humerus the corresponding rotation is clockwise and the twist anti-clockwise. These opposing forces are easily seen to be in operation in the two humeri of *Zeuglodon* and of *Prosqualodon australis*, but is even more obvious in the case of *Prosqualodon davidi*, the fore-limb of which is still to some extent in a state of plasticity. In the zeuglodont humerus the deltoid ridge is prominent and is practically entirely confluent with the anterior border of the bone. The same thing happens in *Prosqualodon* but here all surfaces and edges are rounded off and smooth, a preparation for the condition found in odontocetes of the present day. At the lower end the humerus of *Prosqualodon* is considerably compressed laterally, a condition present in a less advanced condition in the zeuglodont humerus. The lower epiphysis of this bone is missing, but that of the left side has been preserved and is attached to those of the radius and ulna. Although the union in the fossil seems to be fairly close, it is of such a nature as to throw considerable doubt on its being so complete as to prevent all movement between the two divisions of the fore-limb. At any rate, the arrangement is much more primitive than is the case in living whales, for not only are the epiphyses distinct as independently formed ossifications but the articulation between the various bones at this joint is extremely well developed.

*Measurements :*

Left humerus :

greatest length.....	154 mm.
length (without epiphyses) .....	112 mm.
greatest width of shaft .....	72 mm.
least width of shaft.....	57 mm.
greatest diameter of head .....	80 mm.
least diameter of head .....	50 mm.

*The fore-arm.* (Pl. I, fig. 6).—On the right side the radius and ulna are preserved separately but are lacking the epiphyses except part of the upper epiphysis of the ulna. On the left side the bones are complete and are in their natural positions. The respective articulations of the radius and ulna with the humerus meet at an obtuse angle. From this angle the articulation of the ulna rises more steeply and is longer. The radius is much stouter than the ulna and is curved with the convexity forward. A little more than halfway down on this edge is a roughened elevation for muscular attachment (? pronator teres).

*Ulna.*—The anterior edge of this bone is practically straight but at its upper end this edge curves sharply forward. This shape, together with that of the radius, causes the inter-osseous space to be of fairly considerable extent. The posterior border of the ulna is concave and is continued above into the very large



fan-shaped olecranon process. This is very similar to that present in living ziphioids. The radius and ulna, though flattened to some extent, are not completely so, their sections being oval in outline and their anterior and posterior borders rounded.

*Measurements:*

Radius, length (including epiphyses) .....	101 mm.
length of shaft only .....	93 mm.
width.....	42 mm.
Ulna, length along posterior border from upper end of olecranon to lower end of bone, including epiphyses.	125 mm.
length along posterior border from upper end of olecranon to lower end of bone, without epiphyses.	117 mm.
length along anterior edge, including epiphyses ..	90 mm.
length along anterior edge, without epiphyses....	74 mm.
greatest width at lower end of olecranon process .	60 mm.
least width .....	34 mm.

*The carpals.*—These, as preserved, are five in number and take the form in general of rounded nodules except in one instance, where the bone is flattened. There seems to be no doubt that in life the carpals were embedded in cartilage. The metacarpals present are four in number, one of them being incomplete. They are slightly flattened and are all to some extent expanded at the extremities.

*Measurements:*

Anterior carpal, length 39 mm., width 13.0 mm.	
Second     "     "     45 mm.,     "     15.5 mm.	
Third     "     "     41 mm.,     "     14.0 mm.	

A radius and ulna, attributed to *Prosqualodon australis*, and obtained from the Chubut Beds, are contained in the collections of the British Museum (M 7257). They agree very closely with those described above for *P. davidi*, and are probably from the left side. They have almost the same relative proportions as the same bones in *P. davidi* but are somewhat larger. Epiphyses are missing. The interosseous space is a little wider. The olecranon process has been broken off but seemed of the same character as in *P. davidi*.

(f) THE STERNUM.

This is represented by a single piece in the form of a triangular plate, hollow above, convex on the ventral surface. All the sides of the triangle are concave. Articulations are shown for two pairs of ribs, one pair just behind the antero-lateral angles, another pair just in front of the posterior border. Whether the whole sternum consisted of one piece it is impossible to say but it is extremely likely. In no squalodont apparently has more than one bone been found representing the sternum. In this respect the group approaches the Iniidae. The manubrium sterni of *Prosqualodon* in general appearance differs considerably from that attributed to *Squalodon grateloupi* (Van Beneden and Gervais, 1880, pl. xxviii) but has a considerable resemblance to the very mutilated sternum of *Phoberodon arctirostris* (Cabrera, 1926, fig. 15).

*Measurements:*

Greatest width ....	135 mm.
Length (median) ..	107 mm.

III. REMARKS ON THE SKULL OF *PROSQUALODON AUSTRALIS* LYD.  
IN THE BRITISH MUSEUM, LONDON.

This skull was described by Lydekker in 1899 and by him was regarded as belonging to the same species as the skull (in the Museum of La Plata) of which he published a description in 1893. It is registered in the British Museum as M 7249.

Both specimens came from the Chubut Beds in Patagonia.

The London skull (Pl. I, fig. 4), was afterwards examined by Professor Abel who agreed with Lydekker's reference of this specimen to the species *australis*, and, after considering the structure and dentition in detail, published a reconstruction of the skull and lower jaw (1912). Cabrera (1926), after examining the type in the La Plata Museum, had no hesitation in expressing the severest criticisms of Abel's findings. Abel had never seen the type and Cabrera, who had reinvestigated the type, had never had before him the skull, on the examination of which Abel founded his conclusions and his reconstruction. It is, therefore, of the greatest fundamental importance that the skull in London should be re-examined and this I have done, particularly with regard to the length of the rostrum, the dentition and the arrangement of the bones in the vertex and side walls of the skull.

*Length of the rostrum.*—Lydekker, in his second account (1899), speaks of "the extreme shortness of the skull (only a very small portion of the rostrum being missing)". Abel indicates in his reconstruction (1912, p. 5) a quite abbreviated rostrum with the premaxilla ending in a short unexpanded extremity. According to Abel's findings, the length of the rostrum is proportionately much less in *P. australis* than we now know it to be in *P. davidi*. Both Abel and Lydekker, no doubt, have been influenced by the rapidity with which the rostrum of the London skull narrows towards the apex and by the extreme thinness of the maxillae at the place where the jaw is broken off short. It was this latter condition which, no doubt, determined Abel in suggesting the absence of incisors in the upper jaw of *Prosqualodon*. In the skull of *P. davidi* the rostrum is complete, but it shows just as much tendency to taper and it is most fragile and liable to fracture at approximately the region in which, in *P. australis*, the fracture has actually occurred.

The following measurements are instructive :—In both *P. davidi* and *P. australis* the width of the rostrum at the base is 188 mm. At the 7th alveolus it is, in *P. davidi* 172 mm., in *P. australis* 174 mm. There is not likely to be, in the complete skull, any very great difference between the two species as regards the length of the rostrum.

*Dentition.*—Of the dentition of the La Plata specimen, Lydekker says (1893, p. 9): "The three teeth remaining in the jaw have double roots and consequently belong to the molar series; while on each side of them is an empty alveolus, thus indicating that the number of typical molars was five, in place of the seven of *Squalodon*. The sixth alveolus from the hinder end shows, however, an imperfectly divided socket, which may, perhaps, be included in the molar series, thus bringing the number of these teeth to six. The four other sockets remaining in the jaw are quite simple and may be reckoned as premolars". Thus Lydekker believed that the number of molars in *P. australis* was either five or six.



After examination of the second skull, however, Lydekker modified his views considerably, for he came to the conclusion (1899) that "the whole number of teeth did not apparently exceed ten or eleven pairs in each jaw, as against the fifteen pairs of *Squalodon*". True, in 1909, says, in discussing this point, that, assuming that the skull described by Lydekker in 1899 is about as large as the type, "it seems likely that the number of two-rooted molariform teeth in the lower jaw did not exceed ten". As a matter of fact, the type skull of *P. australis* is nearly half as large again as the skull in the British Museum.

Abel accepted True's conclusions as to the number of two-rooted molariform teeth. He says (1912, p. 67), "F. W. True hat die Zahl der zweiwurzeligen, molariformen Unterkieferzähne im Maximum auf zehn geschätzt. Meine Vergleiche und Messungen haben zu demselben Ergebnisse geführt; aus dem Abstand der *in situ* befindlichen Zähne in dem Unterkieferrest des La Plata-Museum in Verbindung mit der Länge des Rostrums des Schädels im Londoner Museum geht hervor, dass keinesfalls mehr als fünf Unterkieferzähne jederseits als 'Backenzähne' anzusehen sind". Further, Abel believed that no incisors, were present in the upper jaw of this whale.

After a detailed examination of the London skull, I can find no evidence to support these statements. As I have pointed out above, there is no need whatever to assume any excessive shortness of the rostrum in *P. australis* and, as far as the upper incisors are concerned, there is no reason whatever to suppose that they were absent. It has now been definitely established by Cabrera that three incisors are present in the complete upper dentition of the type skull of *P. australis*. With regard to the number of molars there is, accompanying the skull in the British Museum, a mandible whose importance in this direction has not yet been recognized (Pl. II, fig. 10). It is from the left side (Lydekker calls it the "right") and is some 233 mm. long. It contains the posterior seven alveoli of this side with a portion of the eighth alveolus from the posterior end.

Lydekker does not describe this mandible, but speaks of and figures a detached tooth (1899, text-fig. 2 a). This, on investigation, proves to belong to the mandible accompanying the skull. Neither Lydekker nor Abel seem to have recognized the great importance of this tooth. As pictured by Lydekker, the tooth shows a crown similar to that of a premolar or molar of *P. davidi*, but the arrangement of the edge cusps suggests that the tooth is a molar. The roots as figured are connected throughout their length by an isthmus and this, if correct, would suggest that the tooth belongs to the premolar series. But the figure is not complete.

The roots of this tooth were found to be broken at the extremities and an examination of the mandible resulted in the discovery of these root ends in the anterior (seventh from the posterior end) alveolus in the mandibular ramus. These roots have been removed and fitted to the tooth, which in its complete form is shown in Pl. II, fig. 11.

The roots are free of the isthmus for some part of their extent and end in open extremities. Further, when the matrix was thoroughly removed, the prominence, which, it is suggested, is a vestigial third root, was brought into view. Comparison of this tooth with the lower series of *P. australis* shows without doubt that it is a molar.

Under these circumstances the lower molar formula of the London skull of

*P. australis* must have been at least seven. It is not possible to be certain of the number of molars which were present in the upper jaw of this skull, but there seem from the appearance of the alveoli to have been no more than six. Cabrera calculates that there were, according to the material available to him, but five molars present in the maxilla on each side and it, of course, is possible that some variation will be found in this respect as occurs in some living species of toothed whales.

The dental formula of *P. australis* can, with these reservations, be given as

$$I. \frac{3}{3}. \quad C. \frac{1}{1}. \quad PM. \frac{4}{4}. \quad M. \frac{5-6}{5-7}.$$

*Structural features of the skull.*—Lydekker has already (1899) given a description of the skull. The general details of skull structure are quite similar to what has been described above for *P. davidi*, but in view of Cabrera's criticisms of Abel's conclusions it is necessary to draw attention to some special points.

On the dorsal side of the skull it is a matter of some importance to record that the parietals do not enter into the formation of the skull roof but are prevented from doing so by the meeting of the supra-occipitals and the frontals. This statement is in direct contradiction to that of Abel who examined this skull. In this respect, Abel claimed for this skull a more primitive place in the cetacean series than it deserves. Cabrera's (1926) recent paper finally settled this question for the other skulls of *Prosqualodon*. In the occipital region of *P. australis* the condyles project as in *P. davidi* and measure 61 mm. greatest length by 35 mm. greatest breadth. The nasals are missing but were apparently more or less similar in shape to those of *P. davidi*, having curved posterior edges and bearing the same relation to the frontals. The mesethmoidal region shows the same interesting condition as is found in *P. davidi*. The lamina perpendicularis is practically identical in shape, being swollen below and narrowing quickly above. As in the Tasmanian species, the olfactory foramina are large openings, placing the olfactory fossa of the brain cavity in communication with the large single external space into which the blow-holes open. Ethmo-turbinals are developed to the same extent as in *P. davidi*.

The vomer has lost its basi-cranial portion but its rostral end is present and forms an extremely wide trough. This groove is evidently wider than it should be, the skull having been slightly crushed in this region. The vomer is visible to a slight extent on the ventral side between the anterior ends of the maxillae.

The palatines are well preserved, but very little of the pterygoids remains. Nevertheless, there is sufficient to show that the median conjoined portion of the palatines was produced backwards in such a way as to prevent the pterygoids meeting to form portion of the median aspect of the hard palate in its posterior region.

*Skull foramina.*—Within the skull can be seen a well-defined groove for the reception of the optic chiasma. The optic foramen runs out from the end of this to unite with the foramen lacerum anterius as in *P. davidi*. On the floor of the cranial cavity can be seen the carotid foramina, although their external openings cannot be found, this part of the skull on both sides having been much broken and repaired. The foramen lacerum medius and the foramen lacerum posterius can be easily made out and have the same position as in *P. davidi*.



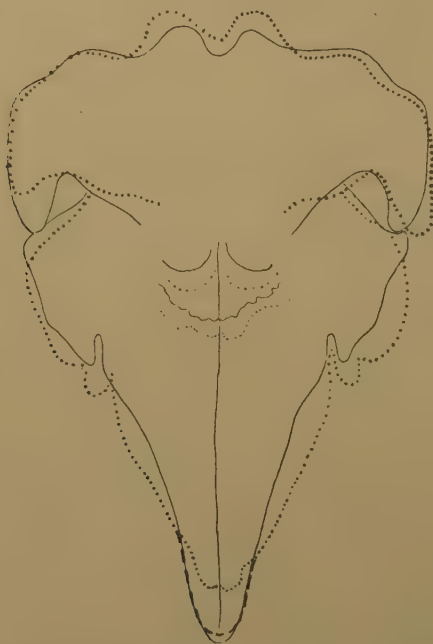
The following are some characteristics of the mandible associated with the skull (Pl. II, fig. 10):—

The symphysis is of moderate length, extending back to the anterior end of the sixth alveolus from the posterior end. The mandible is much weaker than that of *P. davidi*, but shows the same twist, a little less pronounced. The alveoli of the mandible show that the teeth were more separated than in *P. davidi* and that the two posterior molars were much smaller than the others. The antero-posterior axis of each molar was inclined to the longitudinal axis of the jaw in the same way as in *P. davidi*, but it is not possible to say what the direction was in the case of the last molar. The sole remaining tooth is much weaker in all respects than the corresponding molar of *P. davidi*, and is further different in that it stands well out of the jaw. The condition of the roots has already been referred to.

Comparative measurements of the lower anterior molar of  
*P. australis* and of *P. davidi*.

	<i>P. australis</i> mm.	<i>P. davidi</i> mm.
Total length .....	53.0	54.0
Length of roots, anterior .....	35.0	31.0
posterior .....	32.0	30.0
Diameter of tooth, antero-posterior ....	18.0	22.5
transverse .....	11.0	13.0
Crown, greatest height .....	22.0	26.0
least height .....	14.0	21.5

Text-figure 9.



Comparison of the skull contours of *Prosqualodon davidi* and of *P. australis*. (B.M. No. M 7249).

The contour of *P. davidi* is represented by an unbroken line, the contour of *P. australis* by a dotted line. The restoration of the snout of *P. australis* is shown by a broken line.

Text-fig. 9 shows the contours of the skulls of the two species of *Prosqualodon* drawn from the ventral side. It can be seen that the basi-cranial floor of *P. australis* is longer in proportion to its width than is the case in *P. davidi*.

After the above analysis was completed, a tooth was found in the British Museum which bears a label in the late Dr. C. W. Andrews' handwriting as follows:—" *Prosqualodon australis*, Miocene, Patagonia. Belonging to skull exhibited in wall-case ". The skull referred to is the one described above (M 7249). No other information is forthcoming about this tooth. The crown is practically complete but the root is nearly all missing. It appears to be a canine and its ornamentation is much like that of the anterior teeth of *Prosqualodon davidi*. The crown is similarly shaped but is much shorter in relation to its diameter than is the case with *P. davidi*. It bears the same two ridges very minutely denticulated.

*Measurements :*

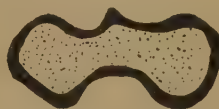
Height of crown (slightly broken at tip).. . . . . 17 mm.  
Diameter of crown . . . . .  $11 \times 10$  mm.

#### IV. REMARKS ON THE MOLAR TEETH OF *PROSQUALODON*.

The presence of an isthmus connecting the two roots is a peculiar feature of the molar teeth of *Prosqualodon*, in which these depart markedly from those of *Squalodon*.

In considering this peculiarity, Abel came to the conclusion that it is a definite specialization and that it represents a considerable advance on the squalodont type, in that it indicates an approach towards the condition in which the two roots are fused to form one, *i. e.*, it forms a stage between the two-rooted tooth found in most squalodonts and the simple rooted tooth of the odontocete of the present day. True (1910, p. 450), in describing a tooth which he considers to be a right lower molar of *Prosqualodon*, states that " on the outer side, between

Text-figure 10.



Horizontal section of the roots of the third lower molar of the left side. ( $\times 1\frac{1}{2}$ ).

the two branches, is a low rounded eminence, like a rudimentary third root ". This phenomenon, as I have shown, occurs in the molar teeth of *Prosqualodon davidi*, and it can be seen in the figures of these teeth shown in Pls. III & IV. In order to see, if possible, what relation this elevation bears to the pulp cavities of the main roots, a section has been taken across one of the molars (the third lower) of *Prosqualodon*, and an outline of the section with the contained cavity is shown in text-fig. 10.

The position of the plane of section can be seen in the photograph of the tooth reproduced in Pls. III & IV. The text-figure shows that the isthmus is hollow and is swollen in its middle portion to form a root-like cavity continuous with that of the main roots. If this cavity can be regarded as a rudimentary third root then, in this respect, the dentition of *Prosqualodon* is more primitive than, in general, is the case in *Squalodon*.



V. THE SYSTEMATIC POSITION OF THE GENUS *PROSQUALODON*.

In spite of its obvious squalodont affinities there has been until recently considerable doubt as to the actual position of the genus *Prosqualodon* in the cetacean series. This was due to Abel's statement made in 1912 that in this genus the parietals together form a band across the vertex of the skull.

As long ago as 1922, Professor D. M. S. Watson and myself thoroughly examined the London skull and it was soon obvious that Abel was in error and that in this particular skull, at any rate, the parietals are prevented by the meeting of the supra-occipital and the frontals from appearing in the skull roof and are confined to the side walls. This discovery was conveyed to Dr. Remington Kellogg, but not in time for it to be of use to him in the preparation of his key to the shark-toothed cetaceans, which appeared in his paper of 1923. Sometime previous to this, Allen had been misled into grouping *Prosqualodon* with such obviously primitive genera as *Agorophius* and *Patriocetus* (Allen, 1921).

That some perplexity existed was evidenced by the statement of G. S. Miller to the effect that, if the parietals formed a broad band across the vertex as described by Abel, this character would show the presence of a stage of telescoping anterior to that present in *Squalodon* and would place the genus *Prosqualodon* in a family of its own (1923, p. 46). The whole matter was definitely settled by Cabrera, for this investigator has examined the type skull of this genus and has shown (1926) that the arrangement of the bones of the side-walls of the skull is of the same plan as in *Squalodon*, the parietals being excluded from the vertex by the supra-occipital and the frontals. The genus *Prosqualodon*, therefore, definitely takes its place among the other genera of the family Squalodontidae.

This family falls more or less naturally into two groups, one longirostral, the other brevirostral. The members of the former, besides being characterized by the possession of a long narrow rostrum with teeth of the squalodont type, have molar teeth whose roots are not joined by any evident isthmus. In the second brevirostral group the teeth are still of the general squalodont type, but the molars possess roots which are either joined throughout their length or are connected by a more or less extensive isthmus. The former group comprises *Squalodon*, *Proberodon* and allied genera, while in the latter, as far as I am aware, would be included only two genera, *Parasqualodon* Hall and *Prosqualodon* Lydekker as follows :—

Genus *Parasqualodon* Hall. Molar teeth with roots joined throughout their length. Roots about twice as long as the height of the crown.

*Parasqualodon wilkinsoni* McCoy.

Genus *Prosqualodon* Lydekker. Molar teeth with roots connected by an isthmus. Roots slightly longer than the height of the crown.

*Prosqualodon australis* Lydekker. Dental formula, so far as is known, probably  $I. \frac{3}{3}. C. \frac{1}{1}. PM. \frac{4}{4}. M. \frac{5-6}{5-7}$ . Molar teeth are well separated from one another and stand out prominently above the alveolar level in the jaw.

*Prosqualodon davidi* Flynn. Dental formula,  $I. \frac{3}{3}. C. \frac{1}{1}. PM. \frac{4}{4}. M. \frac{6}{6}$ . Molars are closely packed and do not stand out prominently in the jaw.

*Prosqualodon hamiltoni* Benham. Dental formula unknown, and no information is forthcoming as to the closeness of the packing of the molars in the jaw. This species, however, is distinguished from the two others by the fact that the supra-occipital bone in its lateral portion forms a distinct ledge 6 cm. wide, overhanging the temporal fossae. A somewhat similar ledge occurs in *Patriocetus* (Kellogg, 1928, p. 182; Abel, 1913, p. 11).

## VI. AUSTRALASIAN REMAINS OF ARCHAEOCETI AND PRIMITIVE ODONTOCETI.

Record of Investigations :—

1867. McCoy describes a molar tooth which he refers to a new species of *Squalodon*, *S. wilkinsoni*.

1867. McCoy refers to this tooth in his Exhibition Essays.

1867. McCoy's Exhibition Essays reprinted in the Annals and Magazine of Natural History.

1875. A further and more detailed description of the above tooth is published by McCoy in the Prodrum of the Palaeontology of Victoria.

1879. A tooth belonging to the anterior portion of the tooth series is described and figured by McCoy and by him referred to the same genus and species as before, *Squalodon wilkinsoni*.

1880. Hector describes under the name *Kekenodon onomata* a tympanic bulla and a number of teeth all discovered in the Miocene of the South Island of New Zealand. *Kekenodon* is obviously an Archaeocete of large size.

1881. E. B. Sanger figures and describes a molariform tooth from South Australia. To this he gives the name *Zeuglodon harwoodi*.

1881. Davis describes a tooth from New Zealand under the name of *Squalodon serratus*.

1908. Stromer suggests that *Zeuglodon harwoodi* is closely related to *Phococetus*.

1911. Hall considers the whole status of Australasian squalodont and zeuglodont remains and includes all but *Kekenodon* in two new genera, *Parasqualodon* and *Metasqualodon*.

1913. Abel puts forward the suggestion that *Zeuglodon harwoodi* should be assigned to Lydekker's genus *Microzeuglodon* and also gives it as his opinion that *M. harwoodi* and *M. causicum* are nearly related to *Neosqualodon*.

1916. Dal Piaz refers to *Squalodon wilkinsoni* from the Australian Miocene beds and says that it is impossible to be able to determine relationships from a single tooth of this kind. He is also of the opinion that the tooth described by Davis is certainly not a squalodont.

1921. Winge states that the genera *Parasqualodon* and *Metasqualodon* as defined by Hall are considered to be nearly related to *Prosqualodon*, but being known only from loose teeth their status is uncertain.

1923. Remington Kellogg accepts Hall's genera *Metasqualodon* and *Parasqualodon* and includes them in the family Squalodontidae.

1928. The above author again puts these genera among the Squalodontidae (with *Prosqualodon*).

1935. Benham, of New Zealand, refers to the genus *Microcetus* Kellogg, part of a lower jaw with six teeth *in situ*, and one loose tooth which were on exhibition



in the Dominion Museum and which had previously been considered as belonging to *Kekenodon onomata* Hector. The new species is *M. hectori*.

1937. Further remains of New Zealand Archaeoceti and primitive Odontoceti are described by Benham:—a zeuglodont (*Lophocephalus parki*), and a new species of *Prosqualodon* (*P. hamiltoni*), the remains of which consists of a fairly complete skull, some teeth, vertebrae, a scapula, etc. In a third paper he records the discovery of some vertebrae, limb bones, etc. of *Kekenodon*.

1942. Benham changes the genus name *Lophocephalus* (pre-occupied) to *Mauicetus*. At the same time certain molar teeth previously referred by him to *Lophocephalus* are now stated to belong to a new species of *Squalodon*, *S. andrewi*. The generic diagnosis rests on the absence of an isthmus between the diverging roots of the molar. If Benham be right in this matter, then this is the first recorded tooth of a true *Squalodon* in the Southern Hemisphere.

#### *Remarks on the above.*

In his very comprehensive paper, Hall (1911) attempts to bring together all the previous descriptions of supposed zeuglodont and squalodont teeth from Australasia, and, with the aid of these and some other teeth and leaving Hector's genus *Kekenodon* (1880) intact, he founded two new genera, *Metasqualodon* and *Parasqualodon*. These, as defined by the author, differ in the proportion of the length of the root to that of the crown, in the amount of union of the two roots of the molars, and in the relative sizes of the "lateral" (=edge) cusps.

The genus *Metasqualodon* includes but one species, founded by Hall on two teeth. One of these is Sanger's molar, the type of *Zeuglodon harwoodi*. But this tooth would seem to be somewhat primitive in its structure. On this point, both Stromer and Abel are in accord, and have suggested that it is closely allied to *Phococetus* and *Microzeuglodon*.

The other tooth, which Hall assigns to this genus and species (his fig. 6), belongs to the collection of the National Museum, Melbourne, and comes from the Mount Gambier polyzoal limestone. Remington Kellogg (1923, p. 20) is of the opinion that "the ornamentation of the enamel crown suggests a closer relationship with *Parasqualodon wilkinsoni*". It is difficult to decide a point like this with such a small amount of material. This tooth resembles McCoy's type of *P. wilkinsoni* in the ornamentation of the crown and (if it be a molar as the strength of the accessory cusps might lead one to suppose) in the closeness of the contact of the two roots. On the other hand, in size and in the number of accessory cusps, Hall's Mount Gambier tooth (his fig. 6) agrees very well with that described earlier as *Squalodon serratus* by Davis (1888, p. 45, pl. vii, fig. 9). This latter tooth comes from the Whiterock River Quarry and is in the collection of the Canterbury Museum, Christchurch, N.Z. It looks as though, when more material is available, it will be found that *Squalodon serratus* Davis and Hall's *Metasqualodon harwoodi*, as exemplified by his Mount Gambier tooth, might be included with McCoy's original type in the genus and species *Parasqualodon wilkinsoni*.

#### *The Genus Parasqualodon.*

Ignoring anterior teeth, which are of little value for diagnostic purposes, the definition of this genus as given by Hall rests also on the appearances presented

by two molar teeth. One of these is preserved in the National Museum, Melbourne, and is the type of McCoy's *Squalodon wilkinsoni* (McCoy, 1867, 1875, fig. 1; Hall, 1911, fig. 5). In some respects this tooth approaches the molars of *Prosqualodon* but the complete union of the roots and their great relative length mark it off definitely from the members of this genus so far described. In many ways it seems to be abnormal and at most is a very unsatisfactory genotype.

The second tooth, ascribed by Hall (Hall's fig. 4) to the genus *Parasqualodon*, comes from the same locality as *Prosqualodon davidi* and resembles the molars of the latter species in general proportions and in the nature of the ornament. On the inner side the crown rugosities are raised into numerous minute cusps. I am indebted to Sir Douglas Mawson for the opportunity of examining this tooth, which is permanently housed in the Geological Museum of the University of Adelaide.

Its measurements are as follows :—

Crown, greatest height .....	30.5 mm.
„ least height .....	23.0 mm.
„ antero-posterior diameter...	26.0 mm.
„ transverse diameter.....	13.5 mm.

The roots are missing.

There is not slightest doubt in my mind that this is a molar of *Prosqualodon davidi*. It bore a manuscript label in Professor Tate's handwriting with the MS. name *Zeuglodon brevicuspidatus*.

As far as the other teeth figured by Hall are concerned I have no difficulty in referring those shown in his figures 2 & 3 to *Prosqualodon davidi*. The tooth in fig. 2 is the second or third incisor, while that shown in fig. 3 is not a premolar, as stated by Hall, but a canine, probably of the lower jaw. The status of the tooth in fig. 1 I leave in doubt.

## VII. *PROSQUALODON* IN ITS RELATION TO CETACEAN PHYLOGENY.

The question of the ancestry and affinities of the Cetacea has recently been the subject of an exhaustive review by Slijper in a comprehensive and outstanding monograph on the group (1936).

This author comes to the conclusion, now apparently fairly universally shared, that the stem-origin of Cetacea is to be found in a primitive Insectivore stock, probably closely related to the Pantolestidae. From such an ancestral group have arisen also the evolutionary lines which gave rise to primitive Carnivores, primitive Ungulates and the more recent Insectivores.

According to Slijper, the original terrestrial Insectivore group probably developed into two main phylogenetic types :—

(a) Short-tailed forms in which the tail is sharply separated off from the trunk. These formed the stem-line of the Archaeoceti and Mystacoceti, the former branching off almost immediately.

(b) Long-tailed forms with the tail not sharply marked off from the trunk. This group gave rise to primitive Odontocetes and from these the Agorophiidae soon separated, leaving the primitive Squalodonts to give rise to the remaining Odontocetes.



According to Slijper, therefore, any affinities which appear to exist between Archaeocetes and Mystacocetes on the one hand, and Odontocetes on the other, are due only to their common origin from an ancient primitive terrestrial Insectivore stock (1936, figs. 252 & 253, pp. 544 & 558).

Such an opinion is not universally held. In particular the position of the Archaeoceti has given rise to a good deal of discussion. Up to 1926, the facts available were so unsatisfactory and the conclusions to be drawn from them so conflicting, that in that year Anthony considered the question practically insoluble. "Quant aux Zeuglodontidae", he says (p. 133), "où faut-il les placer? Peut-être sont-ce des Créodontes adaptés à la vie aquatique, et alors ils n'auraient aucun rapport avec les Cétacés? Peut-être au contraire, dérivant des Condylarthres primitifs font-ils partie du même phylum que les Cétacés?"

Kellogg (1928, p. 41) suggests that there are at least three distinct lines of descent, each leading to one of the three suborders (Archaeoceti, Mystacoceti, and Odontoceti) into which Cetacea are usually divided.

On the other hand, as recently as 1933, Raven and Gregory make the following statement as to their attitude on this matter:—"We are met with the objections of Gidley (1913) and Miller (1923) that the Archaeocetes of the Eocene and Lower Oligocene were not ancestral whales. While this is doubtless true of the excessively specialised *Zeuglodon* and its near relatives, yet the skull of *Protocetus fraas* (1904) of the Lower Oligocene, although perhaps too late in time, points the way unmistakably toward the curious relations of the bones of the snout in both orders of whales".

The question which concerns us here is whether the structure of a primitive Odontocete skull such as that of *Prosqualodon davidi*, excellently preserved as it is, throws any light on the problem of the origin of the Cetacea and the affinities of the various subdivisions of the group.

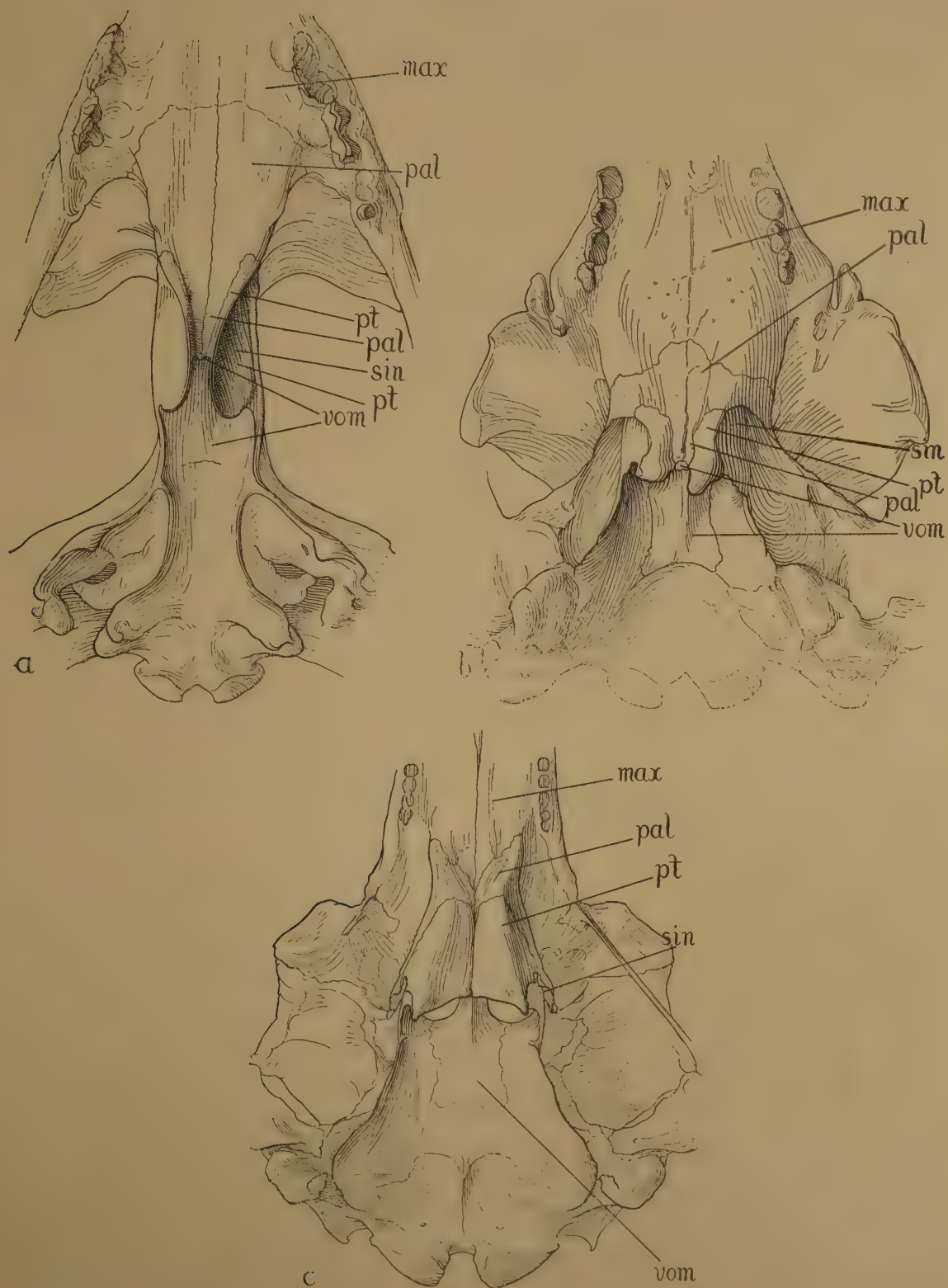
(a) Dart has examined intra-cranial casts of various Archaeoceti and of *Prosqualodon davidi* and compared them (1923). He comes to the conclusion that zeuglodonts are not in the direct line of cetacean ancestry and that *Squalodon* (= *Prosqualodon*) has at least close affinities with the true cetacean stock.

(b) An opportunity has arisen for comparing the structure of the palate of at least one Archaeocete (*Zeuglodon osiris*) with the same region in *Prosqualodon*.

The posterior region of the palate is not often available for examination in fossil skulls of this type, as G. S. Miller regrets, while Anthony, speaking of the skulls of zeuglodonts, says that with regards to this region they "sont presque toujours endommagées ou inaccessibles sur les fossiles".

In *Prosqualodon davidi* (text-fig. 11 (b)) the palate is best developed and is most expanded at a level corresponding with the bases of the antorbital notches and just behind the posterior molars. The expansion here and behind this point is evidently due to the fact that the palate has not recovered from the movement backward of the narial passages and their gradual assumption of a vertical position. The posterior portion of the hard palate is composed of the palatines and pterygoids. The palatines together form a transverse bridge, strongly convex ventrally. They are suturally distinct in the mid-line where each sends back a posterior prolongation. These two processes together entirely separate the two pterygoids. At the apex of this combined extension of the palatines can be seen the end of the keel of the vomer. On each side is the post-palatine sinus, relatively wider and shallower

Text-figure 11.



Comparison of the structure of the palate in (a) an Archaeocete (*Zeuglodon osiris*), (b) a primitive Odontocete (*Prosqualodon davidi*), and (c) a modern Odontocete (*Tursiops truncatus*) (see pp. 188-92). max=maxilla; pal=palatine; pt=pterygoid; sin=post palatine sinus; vom=vomer.

(Drawings by Miss Joyce Townend.)



than in living *Odontocetes* and contained between two walls each formed partly of palatine and partly of pterygoid. The external wall is not very well developed, so that the sinus opens ventro-laterally rather than posteriorly. The posterior, ventrally concave, plate-like prolongation of the vomer is very evident in the figure. As I have already stated, it ends in a prominent ledge and is not closely applied to the cranial floor.

The lower openings of the narial passages or blow-holes are not visible on this inferior aspect of the skull. They have not reached the maximum posterior position.

For comparison a figure is given (text-fig. 11 (c)) of the arrangement of the various parts of this region of the skull in *Tursiops truncatus*.

The palate is here strongly contracted. The blow-holes have reached their final position and direction. The posterior hard palate is formed of palatines and pterygoids. Strong evidence is present of telescoping, the maxillae, for example, having slid over the palatines to a large extent. Some effect of telescoping is also evident in the structure of the pterygoids.

The two pterygoids meet in the midline to produce the hard palate backwards. This is entirely secondary and is, of course, as is well known, not characteristic of all *Odontocetes*. The post-palatine sinus is built on the same plan as in *Prosqualodon davidi*, its walls including both palatine and pterygoid bones, but its outer wall is much better developed than in *Prosqualodon* and its cavity is greatly narrowed from side to side.

The vomerine plate in its posterior prolongation is, as is usual in *Odontocetes*, quite thin and firmly fused to the skull floor.

Anthony (1926) has presumed a great deal of importance for the post-palatine sinuses (as well as other structures) which, as he points out, accommodate diverticula of the Eustachian tube and he states that if the Eustachian diverticula be shown to occur in Zeuglodonts, it would certainly show their close relationship with the Cetacea. At the same time it would indicate that these groups have a closer connection with the Ungulates than with the Carnivores.

It would be of the greatest interest to examine in this respect known Archaeoceti in which the palate is well preserved and of which a detailed survey is possible.

*Protocetus atavus* Fraas is admittedly a type which, though occurring too late in the palaeontological record, approaches most closely what might be regarded as the ancestral cetacean. From our point of view, *Protocetus* is also of note in that the posterior hard palate is more or less complete. Examination of fig. 2 of Tafel 1 of Fraas' paper, shows the presence on each side of the posterior portion of the palate of two depressed areas. Each of these is bounded antero-mesially by a definite ridge and is apparently also limited by a similar but less well-defined ridge externally. It is not possible from Fraas' figures to make out the relationships of palatines and pterygoids in this region, and his description unfortunately is very brief. He says (p. 9), "Die Palatina jedoch greifen noch weit zurück und zeigen in ihrer hinteren Hälfte eine durch eine scharfe Kante markirte Erhöhung, welche in eine förmliche Crista übergeht. In diesem Theile nehmen auch noch die Pterygoide an der Bildung des harten Gaumen theil, indem sie sich seitlich an die Palatina anlegen".

It appears fairly obvious that we have here a condition which could be regarded

as antecedent to that occurring in *Prosqualodon*, which again precedes modern Odontocetes in this respect.

Among the Zeuglodont skulls preserved in the Natural History Museum, London, is one in which the palate in its full extent is quite well preserved. This is the skull (M 10228) of which Dart examined an intra-cranial cast and which both Dart and C. W. Andrews definitely refer without doubt to *Zeuglodon osiris* Dames. In this skull the palatine bones are complete and the pterygoids almost entirely so. Text-fig. 11(a) shows the posterior region of the palate with the slight amount of restoration necessary. It differs a good deal from Stromer's conception of this region (1908, Taf. v (ii), fig. 1). In this connection it must be pointed out that Dart and Andrews have agreed that the description of *Z. osiris* in Stromer's second paper (1908) does not agree with his description of the species of the same name in his earlier paper (1903).

In the London skull of *Z. osiris*, the posterior portion of the hard palate is formed partly by the palatines, partly by the pterygoids. The latter are prevented from meeting in the midline by posterior prolongations of the palatines. Compared with this region in *Prosqualodon*, two important differences are noted: (a) the palate is markedly pointed posteriorly, its maximum lateral expansion being considerably in advance of the level of the similar expansion in *Prosqualodon*; (b) the transverse palatine band is noticeably wider in an antero-posterior direction than in *Prosqualodon*. These differences are due to the fact that the olfactory canals are largely horizontal, opening approximately halfway along the rostrum. There is, therefore, no telescoping present in the skull.

At the sides of the posterior portion of the palate are to be found depressions corresponding, as far as can be judged, in position and structure with the depressions of similar appearance in *Protocetus* and with the post-palatine sinuses of *Prosqualodon*.

These depressions are not deep, but are bounded by definite ridges, dorsal and ventral, each being composed partly of palatine, partly of pterygoid. The ventral ridges like those of *Protocetus* are extremely distinct, the dorsal ones are not so distinct but more so on the left than on the right. The two ridges are continuous in front.

The conditions in this region, as presented, therefore, respectively by *Protocetus*, *Zeuglodon osiris*, *Prosqualodon davidi* and the modern Odontocete, show the progressive growth and establishment of the post-palatine sinus. It is no doubt too isolated a sequence from which to draw any conclusions and the significance of the phenomenon will have to be judged in connection with other bodily structures examined in the same way.

Since the above was written, Kellogg's monumental "Revision of the Archaeoceti" (1936) has appeared. He refers (p. 237) to the pterygoid air sinus which, he says "is conspicuously developed in later archaeocetes, especially in *Dorudon osiris*". He states also that if such a sac was developed on the skull of *Protocetus atavus* "it must have been quite small". Later (p. 187) he mentions in *Dorudon (Zeuglodon) osiris* the presence of the "large pterygoid fossa for accessory air sac . . .". It will be seen that Kellogg's restoration of the palatal surface of *Zeuglodon osiris* (his fig. 79, p. 188) differs substantially from my own (text-fig. 11(a)), but this does not affect the question of the existence of the palatine sinuses.



Further, it might be mentioned that Kellogg has instituted a new species for the second specimen of Stromer's *Zeuglodon osiris*, referred to above. Kellogg now designates it *Dorudon stromeri*.

Further, this gifted author develops still further his thesis of the multi-serial origin of the Cetacea.

(c) COMPARISON OF THE MICROSCOPIC STRUCTURE OF THE ENAMEL IN THE TEETH OF *Zeuglodon osiris* DAMES, AND OF *Prosqualodon davidi* FLYNN. BY J. THORNTON CARTER.

At the request of Professor Flynn, sections have been prepared from fragments of teeth of *Zeuglodon osiris* and of *Prosqualodon davidi* in the hope of finding in the microscopical structure of the enamel some evidence as to their affinities.

As is well known, the micro-structure of the enamel—the arrangement of the so-called enamel prisms—has been employed as a test of affinity, first by Sir John Tomes in his examination of the teeth in the Rodentia (Philos. Trans., 1849), and later by Sir Charles Tomes in "An investigation of the structure of the Enamel in the Creodonta" (Proc. zool. Soc. Lond., 1906, vol. i) in which comparison was made with the enamel of Marsupialia and also of Carnivora.

In later years this method of investigation has been extended by other workers, with the result that it is safe to say that the microscopical structure of the enamel, taken in conjunction with other characters, affords admissible evidence as to affinity. In the great Orders this evidence is conclusive, since there is a striking and obvious difference in the pattern of the enamel in Placentalia, Marsupialia and Multituberculata. On examination of a fragment of the enamel of a tooth from a member of any of these Orders, one can make a definite pronouncement.

In the same way one can identify the enamel of a Carnivore or of an Ungulate, but when it comes to a question of "going back" in geological time and endeavouring to trace remote affinities, much caution should be observed, since many cases of parallelism occur, and it is only with a rather close and complete succession, such as occurs in the ancestry of the Horses, that it is justifiable to express a definite opinion from the histological examination of the enamel alone. With such a reservation, one cannot disregard the value of enamel structure if taken in conjunction with other anatomical characters such as foot structure and brain structure.

Sir Charles Tomes, in his memoir on the Creodonts, points out that—"the enamel patterns of Carnivora are fairly constant . . . the enamel prisms are arranged in bundles, radiating so as to present a goblet form . . . grouped into bundles or sheaves of prisms pursuing an approximately parallel course, whilst towards the exterior of the enamel all the bundles become parallel and straight" (see herewith pl. 5, (a), (b) and (c)). The interglobular layer of the dentine (i-g) is a marked feature. Tomes found that in the Creodonts "the typical carnivorous pattern is not to be found (in *Didymictis*) nor is there any trace of it, so that of the Creodonts examined, this and *Cynodictis* stand alone in this respect".

These observations are significant when it is recalled that Dr. Matthew regarded *Cynodictis* as an example of an early true Carnivore and Tomes states that the "enamel of *Didymictis* differs in respect of its greater simplicity from that of the other Creodonts examined, and from recent Carnivores".

On examination of a section from a tooth of *Zeuglodon osiris* (pl. 5 (d)), the dentine (d) is seen to be of the ordinary fine-tubed variety, not possessing a rich interglobular layer at the amelo-dentinal border. The enamel layer (e) is made up of fine enamel prisms, grouped into "decussating groups of prisms" and preserving such an arrangement almost to the free enamel surface. The layer (s) is interpreted as a deposition of siliceous material during fossilization, a view which is supported by polariscopic examination. Comparison of a section of the enamel of *Zeuglodon osiris* taken at a considerably higher magnification (pl. 6 (e)), with that of an Ungulate (pl. 6 (f)), discloses a close similarity in pattern; whilst comparison with typical carnivore-enamel shows no such resemblance (pl. 5 (a), (b) and (c)). A transverse section of the enamel of *Z. osiris* also shows the arrangement of the prisms into coarse sheaves, which structure persists almost to the surface. The enamel of *Prosqualodon davidi*, though not identical with that of *Z. osiris*, discloses similar features (pl. 6 (g) and (h)) and tends to resemble the Ungulate rather than the Carnivore type of enamel.

### VIII. SUMMARY.

These results may be summarized as follows :—

(a) Dart concludes from his examination of intra-cranial casts that the Archaeoceti cannot be regarded as being on the line of true cetacean evolution.

(b) As far as the structure of the bony palate is concerned, there would seem to be a close resemblance between the Archaeoceti and the Squalodontidae, which may mean a genetic relationship, but on the other hand may be due to their common derivation from a distant primitive mammalian group.

(c) Mr. Thornton Carter's results of the investigation of the microscopic anatomy of the tooth enamel are somewhat surprising. They afford evidence that the Archaeoceti and the primitive Odontoceti are closely related and have ungulate affinities.

These results show how much is still to be learned in connection with this problem, which obviously can only be solved when the palaeontological record is more complete and when all the resources of comparative anatomy (including comparative embryology) shall be bent to the task.

I must express my grateful thanks to the Trustees and Staff of the Australian Museum, Sydney, and of the British Museum (Natural History), London, for accommodation and help given in this investigation.

### IX. REFERENCES.

- ABEL, O. (1912). Cetaceenstudien, iii Mitteilung: Rekonstruktion des Schädels von *Prosqualodon australe* Lyd., etc. *S.B. Akad. Wiss. Wien.* (Abt. 1), **121**, 57-74.
- ABEL, O. (1914). Die Vorfahren der Bartenwale. *Denkschr. Akad. Wiss. Wien.* **90**, 155.
- ABEL, O. (1919). *Die Stämme der Wirbeltiere.* Berlin u. Leipzig.
- ALLEN, G. M. (1921). A new Fossil Cetacean. *Bull. Mus. comp. Zool. Harv.* **65**, 1.
- ANDREWS, C. W. (1906). *A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt.* London, British Museum (Natural History).



- ANDREWS, C. W. (1923). Notes on the Skulls from which the Endocranial Casts described by Dr. Dart were taken. *Proc. zool. Soc. Lond.* **1923**, 648.
- ANTHONY, R. (1926). Les Affinités des Cétacés. *Ann. Inst. Ocean., Paris*, n.s. **3**, 93.
- BEDDARD, F. E. (1900). *A Book of Whales*. London.
- BENEDEN, VAN, & GERVAIS, PAUL. (1880). *Ostéographie des Cétacés vivants et fossiles, etc.* Paris.
- BENHAM, W. B. (1935). The Teeth of an Extinct Whale, *Microcetus hectori*, sp. n. *Trans. roy. Soc. N.Z.* **65**, 239.
- BENHAM, W. B. (1937). Fossil Cetacea of New Zealand, II, III & IV. *Trans. roy. Soc. N.Z.* **67**, 1.
- BENHAM, W. B. (1942). Fossil Cetacea of New Zealand, V. *Trans. roy. Soc. N.Z.* **71**, 260.
- BURLET, H. M. DE. (1913-15). Zur Entwicklungsgeschichte des Walschädels, II & III. *Morph. Jb.* **47**, 645, and **49**, 119.
- CABRERA, A. (1922). *Manual de Mastozoología*. Madrid.
- CABRERA, A. (1926). Cetacéos fósiles del Museo de la Plata. *Rev. Mus. La Plata*. **29**, 363.
- DAL PIAZ, G. (1904). Neosqualodon, Nuovo Genere della Famiglia degli Squalodontidi. *Mém. Soc. paléont. Suisse*, **31**.
- DAL PIAZ, G. (1916). Gli Odontoceti del Miocene Bellunense. Parte seconda: Squalodon. *Mém. Inst. géol. Univ. Padova*, **4**.
- DART, R. A. (1923). The Brain of the Zeuglodontidae. *Proc. zool. Soc. Lond.* **1923**, 615.
- DAVIS, J. W. (1888). On Fossil Fish Remains from the Tertiary and Cretaceous-tertiary Formations of New Zealand. *Sci. Trans. R. Dublin Soc.* **4**, 1.
- FLYNN, T. THOMSON. (1920). Squalodont Remains from the Tertiary strata of Tasmania. *Nature, Lond.* **106**, 406.
- FLYNN, T. THOMSON. (1923). A Whale of Bygone Days. *Aust. Mus. Mag.* **1**, 266.
- FLYNN, T. THOMSON. (1932). A New Species of Fossil Cetacean from Tasmania. *Geol. Mag.* **69**, 327.
- FRAAS, E. (1904). Neue Zeuglodonten aus dem unteren Mitteleocän vom Mokattam bei Cairo. *Geol. palaeont. Abh. n.f.* **6**, 199.
- FENGUELLI, G. (1928). A proposito di alcune incisioni, sull'omero di uno Squalodontidae del Miocene superiore della Patagonia. *Bol. Soc. geol. ital.* **47**, 1.
- GREGORY, W. K. (1910). The Orders of Mammals. *Bull. Amer. Mus. nat. Hist.* **27**.
- HALL, T. S. (1911). On the Systematic Position of the Species of Squalodon and Zeuglodon described from Australia and New Zealand. *Proc. roy. Soc. Vict.* **23**, 257.
- HECTOR, J. (1881). Notes on New Zealand Cetacea, Recent and Fossil. *Proc. N.Z. Inst.* **13**, 434.
- KAMPEN, P. N. VAN. (1905). Die Tympanalgegend des Säugetierschädels. *Morph. Jb.* **34**, 321.
- KELLOGG, A. REMINGTON. (1923). Description of two Squalodonts recently discovered in the Calvert Cliffs, Maryland, and Notes on the Shark-toothed Cetaceans. *Proc. U.S. nat. Mus.* **62**, 16.
- KELLOGG, A. REMINGTON. (1928). The History of Whales. *Quart. Rev. Biol.* **3**, 29.
- KELLOGG, A. REMINGTON. (1929). A New Fossil Toothed Whale from Florida. *Amer. Mus. Nov.* **389**, 1-10.
- KELLOGG, A. REMINGTON. (1936). A Review of the Archaeoceti. *Publ. Carneg. Instn.* **482**.
- LYDEKKER, R. (1893). Paleontologia Argentina, ii. (2) Cetacean Skulls from Patagonia. *An. Mus. La Plata*. **2**.
- LYDEKKER, R. (1899). On the Skull of a Shark-toothed Dolphin from Patagonia. *Proc. zool. Soc. Lond.* **1899**, 919.
- MCCOY, F. (1867). On the Occurrence of the Genus Squalodon in the Tertiary Strata of Victoria. *Geol. Mag.* **4**.
- MCCOY, F. (1867). On the Recent Zoology and Paleontology of Victoria. *Intercolonial Exhibition Essays*. Melbourne.

- McCoy, F. (1867). On the Recent Zoology and Paleontology of Victoria. *Ann. Mag. nat. Hist.* (3), 20, 175.
- McCoy, F. (1875). *Squalodon Wilkinsoni*. *Prodromus of the Palaeontology of Victoria*, Dec. ii. Melbourne.
- McCoy, F. (1879). *Squalodon Wilkinsoni*. *Prodromus of the Palaeontology of Victoria*, Dec. vi. Melbourne.
- MILLER, G. S. (1923). The Telescoping of the Cetacean Skull. *Smithson. Misc. Coll.* 76, no. 5.
- MÜLLER, J. (1849). *Über die fossilen Reste der Zeuglodonten von Nord-Amerika*. Berlin.
- POMPECKY, J. P. (1922). Das Ohrskelett von Zeuglodon. *Senckenbergiana*, 4, 43.
- RAVEN, H. C., & GREGORY, W. K. (1933). The Spermacete Organ and Nasal Passages of the Sperm. Whale (*Physeter Catodon*) and other Odontocetes. *Amer. Mus. Nov.* 677, 1-18.
- RAVN, J. P. J. (1926). On a Cetacean, *Squalodon* (*Microzeuglodon* ?) *wingei*, sp. n. from the Oligocene of Jutland. *Medd. dansk. geol. Foren.* 7, 45.
- RIDEWOOD, W. G. (1922). Observations on the Skull in Foetal Specimens of Whales of the Genera Megaptera and Balaenoptera. *Philos. Trans. (B)*, 211, 209.
- SANGER, E. B. (1881). On a Molar Tooth of Zeuglodon from the Tertiary Beds on the Murray River, near Wellington, S.A. *Proc. linn. Soc. N.S.W.* 5, 298.
- SLIJPER, E. J. (1936). Die Cetaceen vergleich-anatomisch und systematisch. *Capita Zool.* 7, 1-590.
- SMITH, G. ELLIOT (1903). The Brain of the Archaeocete. *Proc. roy. Soc.* 71, 322.
- STROMER, E. (1903). Zeuglodon-Reste aus dem oberen Mitteleocän des Fayûm. *Beitr. Paläont. Geol. Öst-Ung.* 15, 59.
- STROMER, E. (1908). Die Archaeoceti des ägyptischen Eozäns. *Beitr. Paläont. Geol. Öst-Ung.* 21, 106.
- TRUE, F. W. (1907). Remarks on the Type of the Fossil Cetacean *Agorophius pygmaeus* (Müller). *Smithson. Inst. Spec. Publ.* 1694.
- TRUE, F. W. (1910). A New Genus of Fossil Cetacean from Santa Cruz Territory, Patagonia; and a description of a Mandible and Vertebrae of *Prosqualodon*. *Smithson. Misc. Coll.* 52.
- WEBER, M. (1928). *Die Säugetiere*. Zweite Aufl. Jena.
- WINGE, H. (1921). A Review of the Inter-relationships of the Cetacea. *Smithson. Misc. Coll.* 72, no. 8. (A translation with additions by Gerrit S. Miller, Jr. of a paper by Dr. Winge which appeared in Danish in 1918 under the title of "Udsigt over Hvalernes indbyrdes Slaegtskab.")
- ZITTEL, K. A. VON. (1923). *Grundzüge der Paläontologie*, Abt. II.—Vertebrata. München und Berlin.



## X. EXPLANATION OF THE PLATES.

## PLATE I.

- Fig. 1. *Prosqualodon davidi*. Dorsal view of skull. (Photo, Austr. Mus.) ( $\times \frac{1}{4}$ .)  
 Fig. 2. *Prosqualodon davidi*. View of skull from the right side. (Photo, Austr. Mus.) ( $\times \frac{1}{4}$  app.)  
 Fig. 3. *Prosqualodon davidi*. Ventral view of skull. (Photo, T. T. F.) ( $\times \frac{1}{4}$  app.)  
 Fig. 4. *Prosqualodon australis*. Ventral view of the skull (M 7249) in the British Museum. (Photo, Brit. Mus.) ( $\times \frac{1}{4}$  app.)  
 Fig. 5. *Prosqualodon davidi*. Right humerus from the post-axial aspect. (Photo, Brit. Mus.) ( $\times \frac{3}{4}$  app.)  
 Fig. 6. *Prosqualodon davidi*. Left paddle from the internal aspect. (Photo, Brit. Mus.) ( $\times \frac{1}{3}$  app.)

## PLATE II.

- Fig. 7. *Prosqualodon davidi*. Sternum from ventral aspect. (Photo, Brit. Mus.) ( $\times \frac{2}{3}$  app.)  
 Fig. 8. *Prosqualodon davidi*. External view of the right mandible. (Photo, T. T. F.) ( $\times \frac{1}{4}$  app.)  
 Fig. 9. *Prosqualodon davidi*. Internal view of the right mandible. (Photo, T. T. F.) ( $\times \frac{1}{4}$ .)  
 Fig. 10. *Prosqualodon australis*. Internal view of the left mandible. (Photo, Brit. Mus.) ( $\times + \frac{1}{3}$ .)  
 Fig. 11. *Prosqualodon australis*. Molar tooth of left mandible, seen from the lingual aspect, with roots replaced. (Photo, Brit. Mus.) (Slightly greater than natural size.)  
 Fig. 12. *Prosqualodon davidi*. Posterior molar of left ramus of mandible, inner aspect of crown magnified to show ornamentation. (Photo, T. T. F.) ( $\times 3$  app.) (This tooth is depicted from the anterior aspect in text-fig. 8.)  
 Fig. 13. *Prosqualodon davidi*. Posterior view of skull. (Photo, T. T. F.) ( $\times -\frac{1}{3}$ .)  
 Fig. 14. *Prosqualodon davidi*. Right scapula, external aspect. (Photo, T. T. F.) ( $\times -\frac{1}{2}$ .)

## PLATE III.

*Prosqualodon davidi*. The teeth of the left mandible seen from the external (labial) aspect. The third incisor and the second premolar are missing. Reading from left to right, the teeth are as follows:—top row—first and second incisors, canine, first premolar; middle row—third and fourth premolars, first and second molars; bottom row—third, fourth, fifth and sixth molars. (Photo, F. J. Pittock.)



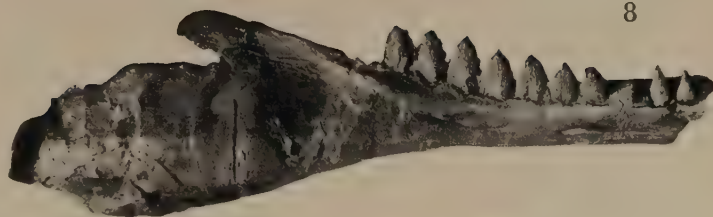




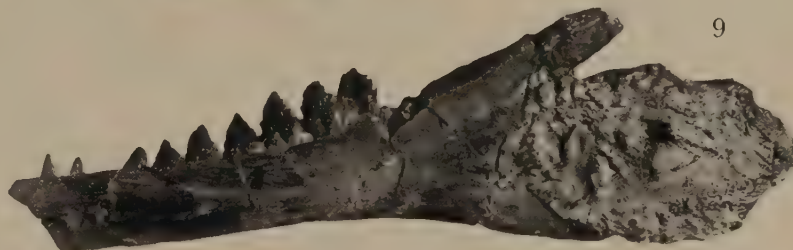
7



8



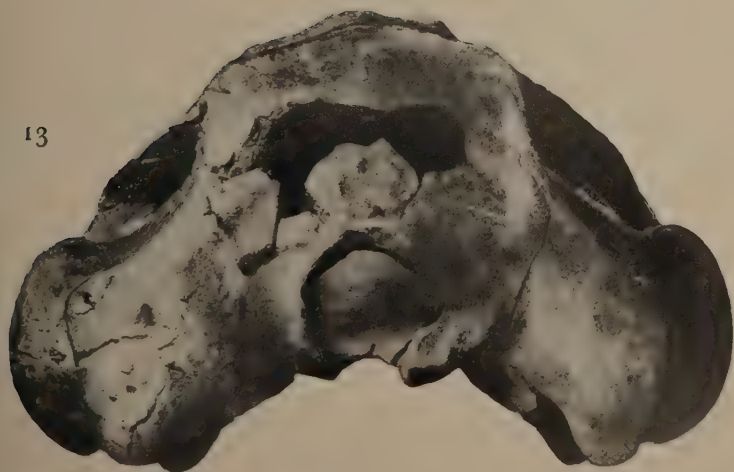
9



10



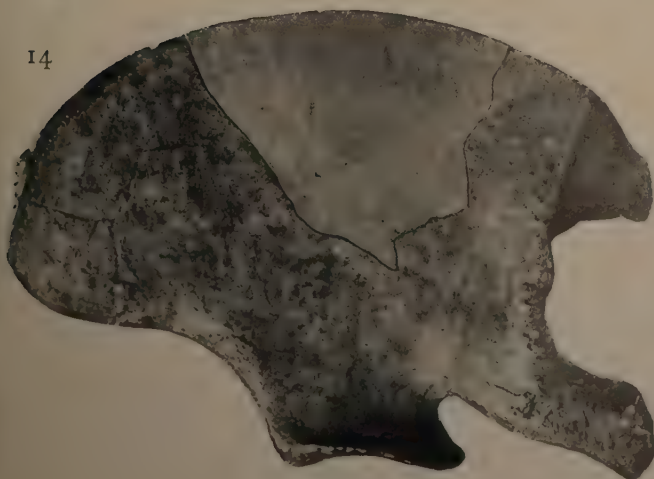
13



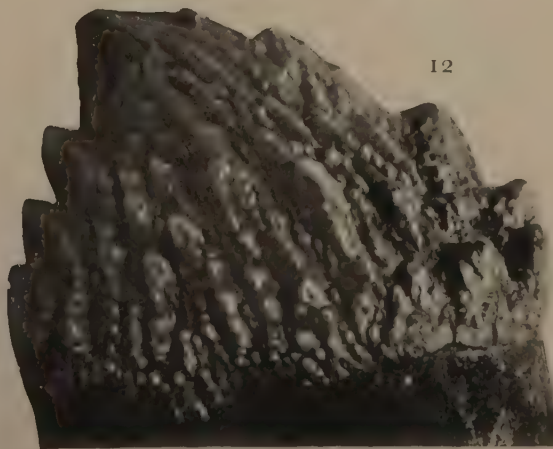
11



14



12









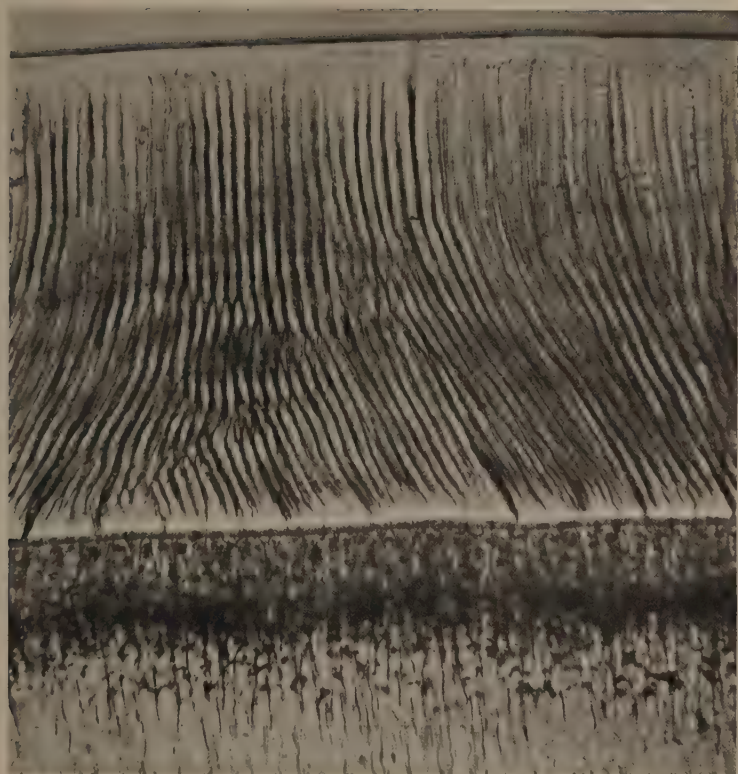




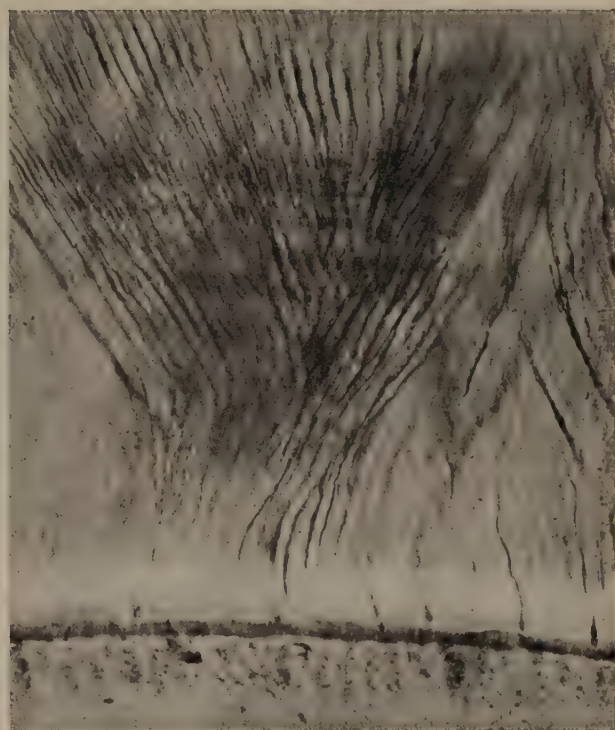








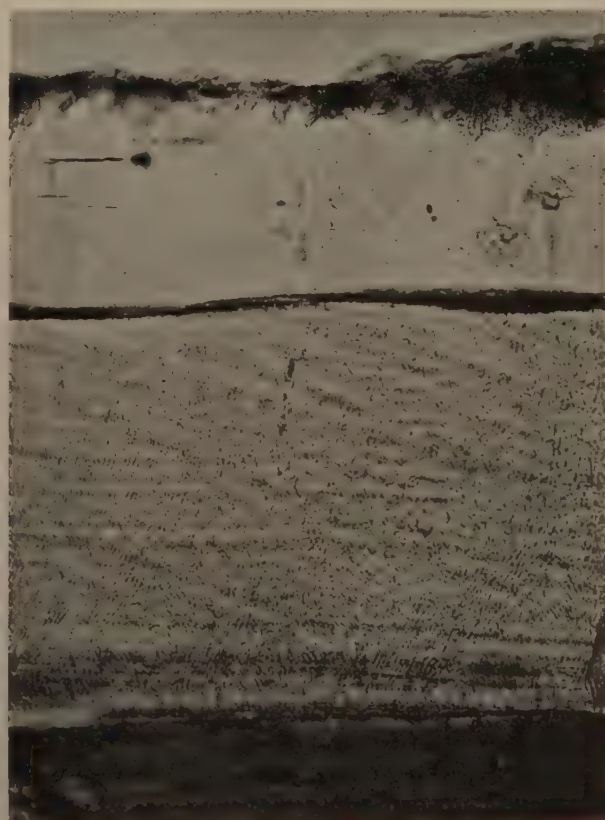
(a) *Felis leo*.



(b) *Otocyon*.



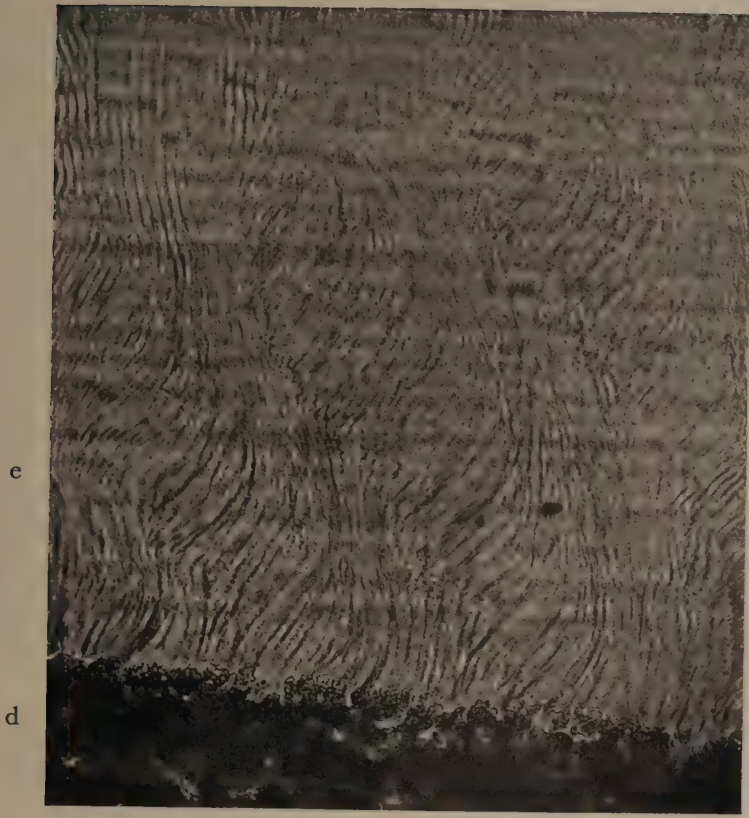
(c) Creodont (*Pachyaena*).



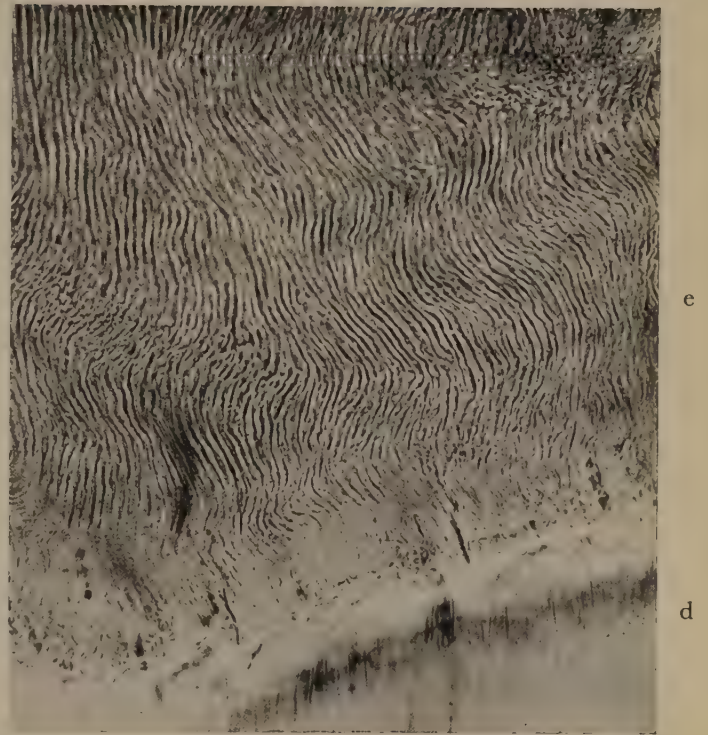
(d) *Zeuglodon osiris*.







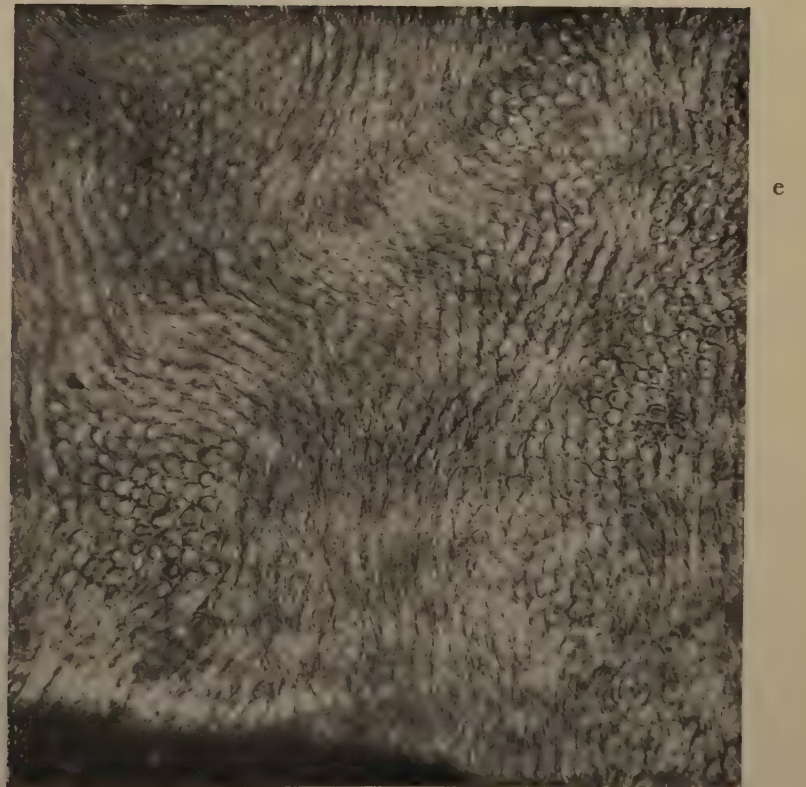
(e) *Zeuglodon osiris*.



(f) Ungulate (*Sus*).



(g) *Prosqualodon davidi*.



(h) *Prosqualodon davidi* (oblique).





*The Caecum of Primates.—Its Appendages, Mesenteries and Blood Supply.* By  
W. C. OSMAN HILL, *Department of Anatomy, University of Edinburgh* and  
R. E. REWELL, *Zoological Society of London.*

(PLATES I–VI.)

[Received March 2nd, 1948.]

The intestines of mammals have been the subject of a number of anatomical studies, more or less complete, and many of their features have been described in some detail, *e.g.* Chalmers Mitchell (1905, 1916). In most cases, however, only the characters of the muscular tube alone when removed from the body have been dealt with, whilst the description appears to have been attempted as an end in itself, little being derived from the facts beyond vague generalizations such as that the gut of herbivores is longer than that of carnivores. From our own experience we have found many of the descriptions to be inaccurate and many instances of wrong identification of the animal described are to be found, even allowing for changes in terminology. Moreover, in most studies no attempt has been made to describe the blood vessels or mesenteries or the relations of the gut to other viscera.

In the Primates, however, more accurate and thorough studies have been made than in most groups and many interesting theories postulated as to the origins of the differences observed. Moreover, considerable attention has been given to the mesenteries, *e.g.* Klaatsch (1892), van Loghem (1903), while Le Gros Clark (1934) summarized the previous knowledge in this field where it threw light on the relationships within the group.

As to the region of the caecum in Primates, several comparative studies have been undertaken, *e.g.* Huntington (1903) and Reider (1936) and these two are of particular value in dealing with the mesenteries and blood supply of the viscus and the origin of these. Numerous studies of single species have been made during the last hundred and fifty years, but the mesenteries and blood vessels are seldom described or figured, even by such masters as Owen (1868) and Beddard (1909 *a*), such aspects as the arrangement of internal folds or constrictions of the gut wall being considered of more importance. We do not seek to belittle the value of the description of such structures, but in the past highly speculative and dubious theories of their function have tended to obscure the facts, even in the minds of the best anatomists, *e.g.* Barclay-Smith (1902), while many of the appearances observed seem to us to have been artefacts due to imperfect fixation in agonal positions, as will be set out in particular instances below. It is, of course, undoubted that the conformation of most of the course of the gut is very different in life and in death, but such things as the length of attachment of a mesentery or the course of an artery must remain constant despite such changes and it is to such facts that we have endeavoured to confine ourselves in the following descriptions. The conformation of a mesentery may be altered by the puckering and shortening of its attachment to the muscular tube, but the actual relations of the attachment remain constant, whether or not the tube relaxes fully in death.



Real interest in the mesenteries and blood vessels of the caecum started with the rise of their practical importance in human surgery, such work as that of Treves (1885) and Keith (1904) anticipating some of the results of Huntington, though without producing the comparative evidence that he did. So good were some of these studies that the work has not been repeated. This is unfortunate, as not only have comparative studies failed to throw new light on this region since that time, but the classic papers often omit variations which we find to be not uncommon and which we submit it might be useful for the surgeon to bear in mind. Certain of even the most recent surgical texts give an account of the anatomy of the region which is far from complete and introduce comparative ideas which are inaccurate and misleading—evidently their authors have neither studied the region themselves in any detail nor read the original papers thoroughly, *e.g.* Love (1947).

Although so important in human surgery, much of the previous work on the appendix lacked any real comparative study of this organ, many sweeping conclusions being based on imperfect series of species. Thus, Barclay-Smith (1902) again considered man's appendix to be an encumbrance and a vestige of the condition found in herbivores, once more on a very inadequate series. On the other hand, Berry (1901) had previously examined several Primates of widely different groups and found the lymphoid tissue of the caecum, from being widespread throughout the wall of the viscus, became collected at its apex and concluded the appendix to be the most complete development of this tendency. It was unfortunate, however, that in his series the animal which showed this concentration most markedly in the absence of a definite appendix was one of the Platyrrhines, which in other respects is highly specialized, then known as "*Midas rufimanus*" and now termed *Mystax midas*, the Red-handed Tamarin. Later it will be seen that our observations confirm those of Berry and re-emphasize the importance of this animal in an understanding of the development of the appendix in phylogeny.

The question of the definition of an appendix thus arises. It is a difficult one and no answer can be attempted at this stage, although it will be discussed more fully hereafter. It is, however, of importance in this paper and, in order to avoid confusion in the detailed descriptions of individual species, the main lines along which we have attempted to attack the question must be indicated now.

From histological criteria, as has been mentioned already, the appendix has been considered to be a specialized concentration of lymphoid tissue, but no evidence appears to exist to show that the functions of this lymphoid tissue, *e.g.* the process of phagocytosis, are any different from those elsewhere in the gut, even in the caecum itself, so that where there is no gross differentiation between caecum and appendix, the latter cannot be distinguished by the structure of lymphoid masses that may be present. The presence of certain types of nerve endings has been emphasized, *e.g.* by Gluckmann (1946 *a*), but no large series of species appears to have been studied. Such special conducting tissue that has been found is situated at the ileo-caecal junction (Keith, 1915 and Hunter, 1936).

That the appendix is an obvious diverticulum of the caecum with a smaller bore is apparent in Man, the great Apes and *Aotes*, but this criterion is of doubtful value in such a genus as *Daubentonia*, a fact which was realized by Owen (1863), who, in his excellent monograph on the Aye-aye, was careful to avoid the conclusion that the sudden narrowing and bending of the caecum indicated the presence of an appendix.

The old test employed by surgeons in searching for the appendix, viz. that at its base the taeniae coli come together to form a complete, thick coat of longitudinal muscle over the viscus, would certainly appear to be of some value. Thus, *Galago* or *Macaca*, in which the caecum is sacculated and possesses taeniae coli, show no appendix, but it must be conceded that this would have been obvious in any case, while the acceptance of such a criterion as absolute would imply that animals in which the caecum has a complete layer of external longitudinal muscle cannot possess an appendix by definition, *e.g.* the Lorisidae. We are not satisfied that such an arbitrary and restrictive definition is useful, but the criterion is of help, especially in deciding the status of an artefact when only one specimen of a species is available.

We consider that the blood supply and lymph drainage of the viscus are of importance. It will be remembered that in Man the main blood supply to the caecum is from the arteries arising from the ileo-colic and passing anterior to, *i.e.* to the morphological dextral side of, the ileum, while the appendix has a separate branch from the ileo-colic passing posterior to the ileum, *i.e.* to the morphological sinistral side. Although this does send a branch to the posterior surface of the caecum, there appear to be no branches from the caecal arteries to the appendix, but there are many points about the final distribution of these vessels which have not yet been fully investigated even in Man. It has appeared to us that in some cases separate regions of the caecum at least can be distinguished by means of this difference in blood supply, and evidence will be submitted to show that these regions may well develop into the caecum and appendix of higher forms. The presence of a separate lymphatic drainage with a lymph node in the mesotyphlon is another feature characteristic of the human appendix, but since most of our material had been fixed for some time, the injection of lymphatics was not possible.

Another feature which we find to be of importance in the phylogeny of this region is the arrangement of the mesenteries of the caecum and its appendages, to which we refer as the "mesotyphlon". As pointed out by Huntington (1903), this consists fundamentally of three folds in Primates. There is first a simple, triangular membrane lying in the angle between ileum and caecum and with a free border. Usually, this carries no blood vessels, or if it does they arise from the dextral or sinistral vessel mentioned above. These arteries in the different species may pass more proximal or more distal to the ileo-caecal junction or may have to bridge a wide or narrow gap according to the angle between ileum and caecum. One or other of the vessels may be the larger, one or other may give branches which run into the anangious central fold described above, and the position is further complicated by the fact that in some species, *e.g.* in Man, the mesocolon is so short that one of the arteries, usually the sinistral, becomes compressed between the gut and the posterior abdominal wall. In the ideal, primitive condition where the arteries are of the same size and the caecum hangs freely in the peritoneal cavity, it will be seen that the arteries running down to the caecum on either side will each raise up a fold of peritoneum, but that the relative sizes and extent of these will be modified by many factors, some of which have been mentioned above. Primarily, however, there are three folds and in the following descriptions it will be seen how all the Primates can be fitted into this scheme despite such extreme modifications in some cases that the original folds may disappear or accessory ones appear. In fact, we find that this



arrangement is not confined to the caecum of Primates, although we are not in possession of the large series of examples necessary to follow this in any other group as yet.

In the following descriptions no attempt has been made to give the relations of the caecum to other structures in the abdomen. Such facts as the descent of its attachment from above the right kidney down into the pelvis as one proceeds from *Tarsius* through the Prosimii have often been described before, *e.g.* van Loghem (1903), and is being described again by one of us (Osman Hill, unpublished). The following descriptions, therefore, concern the caecal region itself and the mesenteries and blood vessels as they are related to the caecum and ileo-caecal junction only, although some attachments to other structures, *e.g.* the colonic labyrinth or ansa coli have had to be included where these help in elucidating the main problem. It will be noted, also, that in deference to the most recent systematists we include the Tupaioidea in the Primates. The classification used is that proposed by one of us (W.C.O.H., 1936 and in "Primates: Comparative Anatomy and Taxonomy", in the Press), but for convenience a few deviations from the strict sequence have been made; these are indicated when they occur.

We have indicated the source of the few species mentioned that we have not examined ourselves.

## I. TUPAIOIDEA.

### 1. TUPAIIDAE.

In *Tupaia* (*Anathana*) *elliotti* (Pl. I, fig. 1) there is a relatively large caecum occupying the right flank. It is at an angle with the colon, which proceeds cranially to a distinct hepatic flexure, as in Man. The ileum joins at an acute angle, but is more in line with the colon than is the caecum. The caecum is similar in calibre to the colon, but is more dilated towards its apex; the longitudinal muscular coat is complete. An extensive vascular mesotymphon connects the proximal two-thirds of the left border of the viscus with the antimesenteric border of the ileum. This duplicature appears to represent an intermediate fold (in Huntington's terminology) fused with a sinistral vessel-bearing fold. The dorsal (posterior) caecal vessels, however, raise a distinct fold, after proceeding beneath the serous covering of the terminal portion of the ileum to obtain access to the mesotymphon. A fossa is formed between this vascular fold and the main mesotymphon. There is, in addition, a rudimentary anangious dextral fold sweeping across the ventral aspect of the gut at the ileo-caecal angle. The ventral caecal artery is small, crossing beneath the serosa proximal to the last-mentioned fold and terminating in the region of the caeco-colic junction. It is accompanied by a tract of adipose tissue. Small lymph glands occur in the mesentery near the ileo-caecal junction.

*Ptilocercus lowii* is apparently more primitive. Le Gros Clark (1926) states that the colon forms a straight tube running directly caudally from the ileo-caecal junction to anal canal fairly close to the mid-line. The caecum is well developed, conical with a faint constriction at the base. Two small lymph glands occur at the front of the ileo-caecal junction and a third lies dorsally. Neither the peritoneal folds nor the vasculature was considered by Le Gros Clark.

## 2. MACROSCOLIDIDAE.

In *Macroscelides rozeti* the large intestine is more specialized than in *Ptilocercus* or *Tupaia*. The ileo-caecal junction lies in the right flank, the terminal segment of ileum being directed cranially. The colon proceeds at a sharp angle, being directed first to the left, then returning on itself, forming thus a short loop or ansa directed to the left. The distal (anal) limb of the loop takes a sinuous course cranially as far as the liver, where another sharp bend occurs to give rise to a short, wide, transverse colon which courses leftwards before finally turning into the straight terminal colon which runs caudally near the mid-line to the anal canal. The caecum is a cylindrical, blunt-ended portion of gut directed cranially to the right of and somewhat dorsal to the first limb of the ansa coli. Its mesentery appears continuous with that of the proximal colon, and no serous connection with the ileum could be detected. The caecum is supplied by branches from the right colic vessels. This arrangement is quite unique and seems to have no relation to that in the Tupaiidae or in Prosimians. The above description differs materially from that supplied by Mitchell (1916), who describes a very simple arrangement of the gut and a much larger caecum.

## II. TARSIOIDEA.

From the point of view of simplicity in the structure of its gut, *Tarsius* may be considered in this place rather than in its true systematic position in the Primate series. Some variations apparently occur among different species of the genus (*e.g.* see Straus (1936)), chiefly due to different degrees of rotation during embryonic life; so that some, *e.g.* *Tarsius philippinensis*, possess a short, transverse colon and others, such as *T. saltator*, do not. In *T. borneanus* (Pl. I, fig. 2) (three specimens examined), we find the ileo-caecal junction placed immediately behind the ventral part of the liver near the median plane. The unsacculated colon courses caudally with but a slight initial sweep to the left. The equally smooth caecum is very long, cylindrical and blunt-ended. It springs from the gut at an acute angle and occupies the cranial part of the right flank. It is provided with an extensive triangular mesotyphlon with an ileal border 10 mm. long and a caecal border 28 mm. long; between the two is a sharp, falciform free border. Like that of *Tupaia* this fold carries the main caecal vessels, which are derived from the superior mesenteric. They proceed subserously across the dorsal aspect of the terminal ileum raising the faintest vestige of a fold as they pass across the ileo-caecal angle near its apex. As in *Tupaia* a ventral caecal vessel proceeds obliquely across the terminal ileum, together with adipose tissue, and ramifies solely upon the ventral aspect of the base of the caecum without anastomosing with the principal caecal vessels. The arrangement agrees thus with van Loghem's description; Reider (1936), on the other hand, reports only a dorsal vessel and peritoneal fold. The caecal group of mesenteric lymph glands lies more proximally than in the Tupaiidae.

## III. CHEIROGALEINAE.

From the point of view of their alimentary tracts the subfamily Cheirogaleinae, as in many other features of their anatomy, show little or no advance on the simple arrangements met with in *Tarsius*. They are, therefore, most conveniently dealt



with at this stage. We have examined two examples of *Microcebus murinus smithii* and one of *Cheirogaleus medius*.

In both genera the colon is simple, lacking the characteristic ansa coli of all the other Lemuroidea. Some mistakes in identification seem to have occurred in van Loghem's material, for this author includes *Galago crassicaudatus* among his series with simple colons, whilst his *Cheirogaleus* is included amongst those possessing the ansa. Quite correctly his *Microcebus smithii* and *Mirza coquereli* (= *Microcebus coquereli*) are listed with simple colons. Beddard (1908 a), too, found *Microcebus* to have a simple colon.

In *Microcebus murinus* (Pl. I, fig. 3), we find the colon disposed much as figured by Reider, but in our examples the ileo-caecal junction had migrated further caudally so as to occupy a position corresponding with that of the human organ. There was, however, no true "ascending" colon, but only a continuous oblique "transverse" colon proceeding directly from the ileo-caecal junction forwards and to the left, where it became continuous with the straight terminal colon by making a wide sweep backwards antero-lateral to the duodeno-jejunal flexure.

The caecum of *Microcebus* is large both in length and calibre. It springs from the ileo-caecal junction at a sharp angle, for the ileum and colon form a continuous tube. In calibre the caecum is equal to the colon; distally it is even wider; its apex is blunt and rounded. No part of the large intestine is sacculated or provided with taeniae. Martin (1835) described the caecum as "somewhat enlarged at its base" with a blunt apex.

The caecum is provided with three mesotyphla, an extensive median or intermediate fold like that of *Tarsius*, and shorter dorsal (sinistral) and ventral (dextral) folds. The sinistral and dextral folds are equally developed and both carry vessels from the termination of the anterior mesenteric artery to the caecum. The median mesotyphlon is anangious, as noted by Reider.

In *Cheirogaleus medius* the arrangements are similar, but the caecum is relatively and absolutely shorter than in *Microcebus* and the dextral vascular fold is better developed than the sinistral. Mitchell (1905) describes and figures a small globular caecum in *Cheirogaleus* (= *Microcebus*) *coquereli*.

#### IV. LORISOIDEA.

This group combines species showing all stages from the simplest form of ansa coli (e.g. *Loris*) to some of the most complex (e.g. *Perodicticus*, Galagidae) and corresponding increases occur in the importance of the caecum.

1. *Loris tardigradus* (Slender Loris = *Stenops gracilis* in van Loghem's account) (see Pl. I, fig. 4).

We have examined seven specimens. The principal advance on the conditions described for the Cheirogaleinae is in the formation of a simple U-shaped ansa coli (Martin, 1833 a). This depends from the region comparable with the transverse colon in Man and is supported by an extension of the mesocolon carrying vessels. Its right limb is also connected to the initial segment of the colon by a triangular anangious fold of peritoneum. This ansacolic ligament, as it has been termed,

has a free caudal border which descends as low on the right as the ileo-caecal junction; on the left it proceeds about half-way along the right border of the right limb of the ansa coli. In spite of the statements of Klaatsch (1892) the colon presents no haustra or taeniae.

The terminal segment of the ileum proceeds cranially to become continuous with the proximal limb of the colon; the junction is somewhat constricted. The large caecum springs from this constricted region at a sharp angle and its commencement is also constricted (? caeco-colic sphincter). It rapidly dilates into a length of gut whose calibre, when distended, is greater than that of the colon. It proceeds caudally and to the left in a uniform curve, the convexity of which is applied to the right flank. It is smooth, thin-walled, unsacculated and has no special vermiform process at its tip. Descriptions of such processes (*e.g.* by Nuhn (quoted by Oppel, 1897; Straus, 1936)) are based upon specimens dying and being fixed in a phase involving peristaltic contraction of the apical segment of the caecum (*vide* p. 221, *infra*). There is no structural differentiation of this region in *Loris*, a fact in which we agree with Broca (1869).

*Loris* possesses but two mesotyphla, a short dextral fold crossing the front of the ileo-caecal angle and carrying a small branch of the ileo-colic artery to supply a limited area of the base of the caecum, and a large intermediate fold connecting the concave left wall of the caecum with the antimesenteric border of the ileum. The latter fold is not, however, anangious. On the contrary, it transports the principal vessels of the caecum, the main stem of which is a direct continuation of the anterior mesenteric which has crossed the back of the ileum subserously to gain entrance to the median mesotyphlon without itself raising a distinct ridge or fold. After gaining the mesotyphlon the vessel runs distally to the caecal apex, gradually approaching the caecal wall. In addition to the caecal branches, some of which form anastomosing loops before gaining the gut, it also gives two branches to the terminal segment of the ileum.

Van Loghem describes the condition of the colon and its mesenteries in an "embryo" *Loris* of 9 cm. C.R. length, in which he found the ansa undeveloped. Since the full-term *Loris*, in our experience, measures only 6 cm. in length and has already a short ansa coli, we suspect that this is another example of erroneous identification. The mistake, however, is not, as might be supposed, due to confusion with *Nycticebus* (which by some earlier writers was also included under *Stenops*), for reasons stated below in dealing with that genus. As a matter of fact the ansa is already developed in foetuses of 5 cm. C.R. length, though relatively the loop is shorter than in the full-term, new-born or adult. We agree, however, with van Loghem as regards the ansacolic ligament, which, in the foetus, is very short, corresponding to the root only of the adult structure. The foetal caecum is, in all respects, similar to that of the adult.

## 2. *Arctocebus calabarensis*.

The gut is known only from Huxley's (1864) account, wherein no reference is made to the ansa coli. Presumably, therefore, it is a simple one, similar to that of *Loris*, which genus *Arctocebus* approaches more closely in many particulars than it does to *Nycticebus* or *Perodicticus*.



Huxley describes and figures a caecum closely resembling that of *Loris*, but much shorter and rather wider in calibre than the colon. A single mesotyphlon is shown, apparently due to the fusion of the sinistral and intermediate folds, for a large vessel is depicted, as in *Loris*, crossing the back of the terminal ileum to gain the mesotyphlon, whence it gives four or five branches to the caecum. Probably a dextral fold is also present, but fresh material of this genus is badly needed.

### 3. *Nycticebus coucang* (Slow Loris). (Pl. I, fig. 5.)

We have examined three adults and a mid-term foetus. Our observations confirm those of Owen, Flower (1872), van Loghem, Harrower (1933) and Reider that this genus has a spirally-coiled ansa coli connected by a thin but extensive serous duplicature with the proximal colon and caecum. The coiling of the ansa is to the right. Taeniae coli were not present in any of our specimens, though both van Loghem and Reider quote examples with a single taenia, Straus one with two such bands and Jacobshagen (1930) one with three.

The caecum is long—relatively and absolutely longer than in *Loris*—of the same calibre as the colon and in line with its commencing limb. It is unsacculated. It differs from that of *Loris* and the Cheirogaleinae in presenting a conical apex. The narrowed region affects the terminal inch of the blind gut and this portion appears to possess thicker walls. It has, in consequence, been described as a vermiform process or appendix (*e.g.* by von Eggeling (1920), Huntington and van Loghem), whilst Straus, in assessing it as grossly homologous to the vermiform appendix of Man and the apes, admits that histologically the homology is lacking. In our opinion the question can only be finally settled by studying the relations of the taeniae in those examples of *Nycticebus* that possess them and by its blood supply. The vermiform termination is, in all our examples, reverted on itself cranially and to the right.

The ileo-colic junction is situated well forwards and to the right, the ileum joining at an acute angle. The caecum thus sweeps backwards and to the left in a semi-circle, occupying the right flank and circumscribing the periphery of the colonic spiral, to the right edge of which it is connected by a broad, anangious, ansacolic ligament. The free edge of this fold extends as far as the junction of the caecum proper with its (vermiform) appendage.

There are three distinct mesotyphla, an extensive median, primarily anangious, triangular peritoneal duplicature extending about an inch along the caecum, and short, symmetrical dextral and sinistral vessel-bearing folds. Sometimes the vascular folds are fat-laden in contrast to the anangious fold, which does not bear adipose tissue, and the same applies to the anangious ansacolic ligament. In two of our specimens a small artery was observed in the free border of the intermediate mesotyphlon derived from the dextral ileo-caecal vessel; it anastomosed, across the dorsal aspect of the ileum, with arteries in the mesentery of the small intestine. In one specimen the sinistral fold carried a vein only. The arrangement of these folds is more generalized than in *Loris* or *Arctocebus* despite the specialization of the rest of the colon.

*A propos* of van Loghem's remarks on pre-natal stages in *Loris*, to which reference has been made (p. 205), it is to be noted here that, in a foetal *Nycticebus* of

51 mm. C.R. length (which corresponds approximately in state of development with a foetal *Loris* of 42 mm.), the characteristic pattern of the colon and its appendages is already manifest.

4. *Perodicticus potto*. (Pl. I, fig. 6.)

Apart from alterations in the relative lengths of different parts of the large intestine, the arrangements in the Potto (six specimens examined) are rather similar to those in *Nycticebus*. The proximal limb of the colon is greatly elongated, causing the ileo-caecal junction to migrate caudally and to the left through a segment of a circle, with the result that the terminal ileum is directed caudally and to the left. The caecum, bent back on itself like the terminal segment in the Slow Loris, occupies the left iliac fossa. The proximal limb of the colon, much elongated and dilated, courses through three-quarters of a circle to end in a flexure situated caudal to the margin of the spleen. From this flexure a U-shaped ansa is directed caudally and to the right, and only slightly bent upon itself dextrally. The elongated proximal limb of the colon would appear to compensate for the simplified ansa. Whereas, however, the caecum and enlarged proximal limb of the colon are smooth-walled and only feebly sacculated, the ansa possesses taeniae and haustra. The taeniae are two in number, one dorsal and one ventral, and are broad, ill-defined bands, the resulting sacculations being shallow and indistinct. The right aspect of the ansa is connected to the proximal limb of the colon and to the caecum by an extensive avascular serous membrane that hides from view the ileo-caecal junction. In the figure the caudal part of the membrane has been removed to expose the ileo-caecal junction and neighbouring structures.

The caecum is relatively short, tapering and with a thickened apex bent back upon itself as in *Nycticebus*. It is in line with the colon and shows no constriction at its base. Like the proximal colon, it is sometimes provided with a complete investment of longitudinal muscle fibres, but in some individuals a single lateral taenia occurs, with consequent sacculations. The taenia lies medial to the line of attachment of the caudal extent of the ansacolic "ligament".

There are but two mesotymphla, intermediate and sinistral. The former is the smaller and extends but a short way along the left border of the caecum, being quite avascular. The sinistral fold extends about half-way along the caecum and carries the posterior or principal caecal vessels. These run subserously over the distal half of the organ. The anterior caecal artery is a very small vessel crossing the termination of the ileum subserously and ending on the adjacent part of the caecum without raising a definite fold and forming no anastomosis with the principal vessels.

The above account differs in several respects from previous descriptions of the same parts. Thus, Mitchell (1905) depicts a double ansa in *Perodicticus*, whilst Reider, following van Loghem, illustrates a spirally-twisted ansa like that of *Nycticebus*, but shows no taeniae or sacculations on any region. He does, however, refer to a single taenia on the lateral aspect of the caecum, such as we found on one of our specimens. Reider also figures accurately the ansacolic ligament, but his



estimate of the mesotyphla is confusing. This author is strongly of opinion that the terminal thick-walled portion of the caecum is macroscopically a vermiform appendage, for he found it in five specimens. It does at least have a blood supply homologous with that of *Homo*.

5. *Galago crassicaudatus*. (Pl. II, fig. 7.)

The general disposition of the colon and caecum of this species have been considered by Flower (1872), Duckworth (1904, subsp. *garnettii*), Mitchell (1905), Beddard (1908 *a*), van Loghem and Reider. All are agreed on the presence of a more or less spirally-coiled ansa, the apex of the loop being to the right. Flower's and Duckworth's figures, show a relatively short ansa, Duckworth's being scarcely more than the simple sigmoid arrangement occurring in *Lemur*.

Our observations are based on two specimens of *G. crassicaudatus argentatus*. Both have the ileo-colic junction situated well forwards on the right side of the abdomen. From its commencement the colon curves over to the left and then backwards to form the proximal limb of a greatly elongated ansa. This is basically U-shaped, but with the U bent on itself in the middle so that its apex points forwards and to the right and overlies the more proximal parts of the colon as in *Nycticebus*. The caecum proceeds caudally from the ileo-colic junction and is in line with and of the same calibre as the proximal limb of the colon.

The caecum is much longer than in *Perodicticus*, and is somewhat narrowed at its apex, where it tends to bend over on itself once or twice. We do not find the short caecum with bloated base sharply contrasted with narrow vermiform apex depicted both by Flower and Duckworth. We find no taeniae nor true sacculations.

The ansacolic ligament is shorter and narrower than in *Nycticebus* or *Perodicticus*, descending about one-third the distance along the lateral surface of the caecum. This species is peculiar in possessing an extensive dextral mesotyphlon arising from the ventral aspect of the lowest portion of the mesentery of the ileum, sweeping over the surface of the latter to attach itself to the medial wall of the caecum. It extends as far distally as the free border of the ansacolic ligament, and like it is avascular. Beneath it, separated by a deep fossa, is a more extensive sheet of membrane carrying the (posterior) caecal vessels. This appears to be produced by fusion of the intermediate and sinistral mesotyphla, the last-mentioned bringing in the large caecal vessels from behind the terminal ileum. Whilst coursing across the ileum subserously the vessels raise a peritoneal ridge, but not sufficiently to produce a fossa.

6. *Galago senegalensis*. (Pl. II, fig. 8.)

The smaller Galagos possess even more complicated large intestines than the larger species. We have examined two specimens of *G. senegalensis braccatus* and three of *G. s. moholi*. In both forms the ansa is still further elongated, sufficiently so to be bent upon itself twice, the coils proceeding over to the right and ventral to the ileo-caecal region. The caecum of *G. moholi* was described and figured as long ago as 1849 by Smith, from whose account Owen (1868) evidently took his data. These authorities depict a long, puckered caecum, the puckering being said by Owen to be caused by the "mesenteriole".

We find the caecum to be a very long, curved tube sweeping backwards and to the left from an ileo-colic junction occupying the right flank. It is capacious, in line with the colon and provided with well-defined true haustra produced by the presence of three broad taeniae, situated respectively on the dorsal, ventral and medial aspects of the gut. Sacculations are continued to the extreme apex of the caecum, so that the vermiform appendage is lacking. Sacculations are also continued aborally for some distance along the colon, but not into the looped portion.

There is no ansacolic ligament in *G. senegalensis*. There are two well-developed mesotyphla, intermediate and sinistral; whilst a third dextral fold is incipient. The intermediate mesotyphlon is the most extensive, having an ileal border 28 mm. long and a caecal border of 60 mm.; this last extending practically to the caecal apex. The free border is falciform and measures 40 mm. The principal (posterior) caecal vessels are carried in a broad falciform sinistral fold, separated at first from the intermediate fold by a deep fossa. About 10 mm. beyond the ileum the vessels enter the intermediate fold which transmits them to the caecal apex, branching off in the manner depicted in fig. 8, where it will be noted that ramifications proceed to the antimesenteric border of the ileum as well as to the caecum (by a system of arcades). The anterior caecal vessels are transmitted in a low fold across the terminal ileum and the artery forms a loop with the most proximal branch from the posterior caecal vessel.

#### 7. *Galago alleni*.

Reider depicts this species with a simple lemurine ansa coli quite different from that of the other Galagos. He also shows a capacious sacculated caecum. In a specimen (B.M. No. 1374 M) we examined, the ansa is not simple, but long and bent once upon itself to the right much as in *G. crassicaudatus*. It is connected with the proximal limb of the colon by a short ansacolic ligament which passes caudally as far as the ileo-colic junction. The caecum is long, capacious and tapers very gradually to a rounded apex; it is incipiently sacculated, its antimesenteric wall being crenulated, but like the colon, it has no well-defined taeniae. The caecum is supplied chiefly by a sinistral vessel that descends behind the ileum in a strongly marked sickle-edged fold, which joins distally the intermediate mesotyphlon. The last-mentioned fold distributes the vessels by a series of arcades to the caecum. A deep sinistral recess proximally separates the two folds. The dextral vessel is confined to a short plica vasculosa which is insufficiently raised to produce a peritoneal fossa. This vessel anastomoses distally with a recurrent twig from the first branch of the sinistral artery.

#### 8. *Euoticus elegantulus*. (Pl. II, fig. 8 a.)

This curious Galago has not hitherto been examined. We have dissected two specimens, both of which agree in possessing a very complex caeco-colon. The colon is sacculated throughout and bears three well-marked taeniae. The ansa is coiled to the right and connected to the "ascending" limb by an ansacolic ligament. The ileo-caecal angle is very acute, the caecum descending in line with the proximal limb of the colon. The caecum is extremely long, coiled and very capacious. It is



very sharply demarcated from the colon, whose taeniae are not traceable onto it. Distally it narrows gradually at first, but more rapidly in its terminal third which appears to be permanently narrowed to form a vermiform appendage that does not dilate when the rest of the colon is artificially distended. The last half inch of this is sharply recurved and held in this position by the mesotyphlon. The caecum is connected to the ileum by an extensive mesotyphlon carrying the vessels to the blind gut. These are derived from both dorsal and ventral caecal arteries which cross the terminal ileum in short fatty folds. The anterior vessel is the smaller. It supplies a limited area of the ventral wall of the caecum and contributes an anastomotic branch which links up with the first branch of the larger dorsal vessel in the mesotyphlon. Other branches of the dorsal vessel are distributed as shown in the figure (Pl. II, fig. 8a) an arrangement which recalls that observed in *G. senegalensis*. The mesotyphlon would thus appear to be fundamentally the intermediate fold that has received vessels secondarily from recession of the vascular folds.

#### 9. *Galagoides demidovii* (*Hemigalago demidovii*).

We have examined four specimens and find the colon of this primitive species resembles that of *Galago crassicaudatus*, having an elongated ansa bent at least once on itself. The bending, however, is sinistral not dextral. Its detailed windings differ individually. There is a distinct "ascending colon" the ileo-colic junction being placed well caudally. Opposite the junction the wall of the tube bulges laterally, but whether this part of the wall is to be considered part of the caecum or simply as colon is undecided. There are no sacculations or taeniae on the colon. The caecum is long and extremely capacious for the size of the animal. Distally it dilates instead of narrowing as is more usual. The tip is upturned, blunt and rounded. This part of the gut presents incipient sacculations.

A broad intermediate mesotyphlon extends as far as the origin of the terminal upturned caecal apex and its ileal border is but little shorter than its caecal attachment. It is separated dorsally at its base from a triangular sinistral fold by a deep sinistral ileo-caecal recess. The sinistral fold transmits the dorsal caecal vessels into the intermediate mesotyphlon, which carries them to the apical region of the caecum. Ventrally a well-marked dextral fold crosses the ileo-caecal junction from a proximal attachment on the dextral leaf of the mesentery to a distal one on the base of the caecum. It transmits a small ventral caecal artery as in *Loris*. As in *Galago senegalensis* the ansacolic ligament is lacking.

### V. LEMURINAE.

With the subfamily Lemurinae (*Lemur*, *Haplemur*, *Lepilemur*) we revert to forms with a simple sigmoid colon, the caudal loop of the S being constituted by the ansa.

#### 1. *Lemur*. (Pl. II, fig. 9.)

The splanchnology of many species of the genus *Lemur* has been described by several authors, notably by Klaatsch (1892), Duckworth (1904), Mitchell (1905, 1916), Beddard (1908 b), van Loghem and Reider.

The species generally reported on are *L. fulvus* (usually under the erroneous title

*mongoz*, but sometimes as *L. brunneus*), *L. macaco*, *L. catta* and *L. variegatus*. Some differences have been noted between these species, whilst individual variations have also been recorded.

In all the general plan is that the colon is very capacious, much wider in calibre than the small intestine, provided with a long, equally capacious but terminally conical caecum and with a simple U-shaped ansa not bent upon itself. The ileo-colic junction is in the right flank, whence the proximal colon slopes forwards and to the left to what Klaatsch terms the right colic flexure, situated caudal to the spleen. As the oral limb of the ansa, it reverts backwards and to the right, returning as the aboral (anal limb of van Loghem and Reider) to the left of the oral limb and making its final flexure in the left hypochondrium before proceeding as rectum.

We have confirmed this arrangement in adults of *L. fulvus* and *L. coronatus* and in new-born specimens of *L. fulvus* and *L. catta*. We note that the colon is relatively smaller in the new-borns and tends to have its apical, narrow portion spirally twisted clockwise on its own axis. The caecum is in line with the colon and is unsacculated and usually without taeniae, though Straus reports two and occasionally three, whilst van Loghem describes a *L. macaco* with as many as four on the proximal colon and the oral limb of the ansa.

Regarding peritoneal folds, *Lemur* has a relatively short, narrow ansacolic ligament extending caudally as far as the ileo-colic junction and therefore not connected with the caecum. The caecum has in *L. fulvus* representatives of all three mesotyphla; the dextral fold is short, thick and tends to be fat-laden. It carries a small anterior caecal vessel which, in the foetus, crosses the ileo-colic junction subserously, only forming a raised fold in later life. The intermediate fold is relatively short, anangious, without adipose deposit and extremely thin. It fuses distally with the longer vessel-bearing, sinistral mesotyphlon which extends distally almost to the caecal apex.

## 2. *Hapalemur*.

The alimentary canal and its appendages in this genus have been considered by Beddard (1884, 1891, 1901). The two species *H. griseus* and *H. simus* differ, according to this author, in the peritoneal relations of the caecum. In *H. griseus* the intermediate anangious mesotyphlon is lacking, but the dextral and sinistral folds are present as in *Lemur*; Beddard suggests that the loss of the median fold is correlated with the shortening of the caecum, but since *H. simus* also has a short caecum, yet retains the median mesotyphlon, this explanation fails.

## 3. *Lepilemur*. (Pl. III, fig. 10.)

The arrangements in this genus are known only from the figures published in Milne-Edwards and Grandidier's Atlas (1890), the text to which never appeared. It is difficult to interpret these figures in terms of present requirements, but the following points are noteworthy. The colon has a simple U-shaped ansa as in *Lemur*. The caecum is very capacious and twisted spirally two and a half turns; its calibre is greater than that of the colon, but it narrows uniformly to a conical apex. It is unsacculated and without taeniae. The figure depicts but one extensive mesotyphlon carrying a large vessel that has descended from the anterior



mesenteric dorsal to the ileum. The peritoneal duplicature should, therefore, probably be regarded as produced by fusion of originally separate sinistral and intermediate mesotymphla. No vessel is depicted crossing the ventral aspect of the ileo-caecal junction as in *Lemur*, the proximal part of the caecum being supplied from the first branch of the principal (dorsal) vessel. This branch also supplies a recurrent twig along the aboral segment of ileum on its ventral face.

## VI. DAUBENTONIIDAE.

Although aberrant in so many other respects the Aye-aye (*Daubentonia*) differs but little from *Lemur* in regard to its large intestine. Though regarded by some (e.g. Schwarz, 1931) as derived from a primitive Indrisoid stock, *Daubentonia* has not, in its gut, followed their evolutionary trends. It may, therefore, be most conveniently dealt with at this point. Its visceral anatomy has been discussed previously by Owen (1863), Peters (1865), Beddard (1908), Mitchell (1916) and Reider. We have examined the isolated, injected viscera of a single example in the Royal College of Surgeons' Museum.

There is a simple U-shaped ansa coli as in *Lemur*, but it is unconnected to the proximal ("ascending") colon by an ansacolic duplicature. Its two limbs are closely connected by a narrow fold carrying a colic branch of the anterior mesenteric artery (Pl. III, fig. 11). Another colic vessel crosses the beginning of the colon transversely and ramifies over the neighbouring gut and base of the caecum. It is crossed obliquely by a slight peritoneal fold as it leaves the mesocolon.

The caecum is elongated, with a bulbous basal portion in line with the colon, and long, tapering distal portion bent sharply at right angles to this and simulating a vermiform appendage (shown well by Owen, 1863). Both parts are provided with a complete longitudinal muscular tunic and present no sacculations. Beddard's figure indicates a longer dilated basal portion and a shorter apical portion than ours, evidently due to different states of contraction of the circular muscular coat.

We find but two mesotymphla, unless the above-mentioned oblique duplicature over the ventral colic vessels represents the otherwise absent dextral fold. The intermediate anangious fold is short, crescentic and separated from the immense sinistral fold by a deep fossa. The sinistral fold carries the caecal vessels as far as the tip of the caecum and may, as in *Lemur*, represent in its distal part a divorced element of the originally more extensive intermediate mesotymphlon.

## VII. INDRIIDAE.

As shown by Milne-Edwards (1875) and by van Loghem, the members of this family present the most advanced specializations in their large intestines, the three known genera (*Indri*, *Avahi* and *Propithecus*) each being modified in its own special way. The chief peculiarities are the great elongation and complexity of the caecum and the inordinate elongation and labyrinthine arrangement of that part of the colon derived from the ansa.

### 1. *Propithecus*.

Our studies are based upon examination of a foetus (106 mm. C.R.) of *Propithecus diadema* (Pl. III, fig. 12). Though simpler in arrangement of the colon

than in the adult (as previously noted by Milne-Edwards) the colon already, in our specimen, exhibits a labyrinth occupying the right hypochondrium caudal to the right lobe of the liver—in contrast to van Loghem's 10 cm. *Propithecus*, which is said to be "very primitive", with an arrangement corresponding to that of *Stenops* (i.e. *Loris*). It is clear that all van Loghem's statements on foetal or embryonic material must be taken with caution.

The labyrinth forms a more or less compact mass, the various coils being held together by peritoneal investments carrying blood vessels to and from the mass. It is succeeded by a "floating" colon which becomes continuous with the rectum without special demarcation.

The caecum is very long, and in the foetus at least, coiled spirally on its own axis, the coils twisting round the mesotyphlon and its contained vessels. It is in line with the "ascending" colon and is of similar calibre, but gradually narrows to a conical apex. Unlike the colon the caecum is sacculated, the sacculations being evidently more pronounced in the adult judging from Milne-Edwards and Grandidier's figures, which depict two narrow taeniae on the ventral surface, and there was presumably at least one more on the dorsal side. In the adult, too, the calibre of the caecum exceeds that of the colon, and its haustra are very voluminous. The organ contracts more suddenly distally to end in its sharp conical apex. But a single mesotyphlon appears to be present with a short ileal and a very long caecal border. This is fundamentally the intermediate, originally anangious, fold that has received the dorsal caecal vessels from a plica vasculosa (representing the sinistral mesotyphlon) across the back of the ileum. The base of the caecum is supplied subserously by a small branch of the dorsal vessel and takes an arched course over the ileo-colic junction to gain the ventral aspect of the caecum, giving off a twig to the ventral surface of the ileum as it descends (cf. *Lepilemur*, where the same effect is brought about by a branch from the opposite side of the ileum).

## 2. *Avahi*.

Judging from Milne-Edwards and Grandidier's account and figures, the general arrangement of the colon and caecum closely resembles that found in *Propithecus*. The labyrinth is said to be somewhat less elaborate. The proximal colon is in direct line with and the same calibre as the caecum; taeniae are continued on to it from the latter. The caecum is similar to that of *Propithecus* and is thrown into about five flexures; it is provided with two taeniae, one dorsal and one ventral, throughout its length, and the haustra are even better marked than in *Propithecus*, at any rate in adults.

A single extensive mesotyphlon is present, resembling that of *Propithecus*, but its contained vessels are more complicated, there being a larger number of smaller branches from the principal dorsal caecal arterial trunk, including one breaking-up into a leash of small vessels to supply the antimesenteric border of the distal ileum. The base of the caecum is depicted with a vessel crossing the ileo-caecal angle ventrally, though no plica is shown.

## 3. *Indri*.

The major part of the intestine in this genus is, according to Milne-Edwards and Grandidier, more dilated than in the other two genera of Indriidae, but the caecum



is exceptional in being relatively narrower as well as smooth-walled and unprovided with taeniae. Its apex narrows gradually to a rounded tip. The colon does not form a spiral, but is disposed in a series of loops superposed like the leaves of a book and connected with each other by peritoneal folds into a heavy compact mass, occupying the right hypochondrium. The mesotyphla are not described and not well-figured, but a very extensive vessel-bearing membrane is depicted in Plate 103-104 of the Atlas and corresponds apparently to the single mesotyphlon of *Propithecus* and *Avahi*. Instead of a single long principal caecal vessel there appears to be a short trunk, soon breaking up into groups of leashes of fine vessels and also giving off similar groups collaterally to the caecum in its passage through the mesotyphlon. A single group also proceeds subserously, without raising a fold, across the ventral aspect of the ileo-caecal junction to supply adjacent parts of colon and caecum.

### VIII. PLATYRRHINI.

Variations in the arrangement and connections of the large intestine, particularly of the caecum and its appendages, are as great among the Platyrrhini as they are among Strepsirhini. Curiously, however, simpler and more primitive conditions prevail among certain of the Cebidae than among the Hapalidae. The marmosets are usually regarded as the most primitive of American Primates, but this certainly does not apply to their alimentary organs. On the other hand, *Saimiri*, an otherwise typical Cebid, possesses a simpler colon than *Tupaia* or *Tarsius*, whilst the primitive *Aotes* has a more advanced colon but its caecum is provided with a true appendix.

#### 1. HAPALIDAE.

The following species have been examined by us :—

*Hapale jacchus*, *H. santaremensis*, *H. argentatus*, *Mystax midas*, *M. imperator*, *Leontocebus leoninus*, *Oedipomidas geoffroyi*.

*Mystax midas* (Pl. III, fig. 13) seems to us to present the most generalized condition of all the above, and may therefore be taken as a type with which the rest may be compared.

The colon describes a simple inverted U-shaped contour commencing in the right flank, sweeping past the caudal aspect of the liver and turning back towards the rectum. It is smooth-walled, unsacculated, showing merely peristaltic dilations at intervals; there are no taeniae, but a continuous, fat-laden mesentery is present throughout.

The caecum is of moderate length, shorter than in any Strepsirhine, except *Hapalemur*; it is cylindrical in form, of similar calibre to the colon, but rather thick-walled, especially towards its apex. It takes a slightly curved course backwards and medially, ends in a rounded, blunt apex and presents a few scattered nodules on its walls. These are probably lymphoid nodules, since Berry (1900), who reported on the histological structure of the organ in this species (under the name *Midas rufimanus*), found lymphoid nodules throughout the caecum, but in greater concentration towards the apex (*vide supra*).

The caecum is connected to the ileum by a short, triangular, intermediate mesotymphon which is transparent and anangious. This fold is in strong contrast with the dextral and sinistral fat-laden duplications which flank it symmetrically, both of which are connected proximally, across the end of the ileum, with the distal part of the mesentery and which distally extend almost to the tip of the caecum. The principal caecal vessels run in the dorsal (*i.e.* sinistral) fold, but presumably a small anterior caecal artery occupies the dextral fold to account for its being the site of adipose deposit. The last-mentioned vessel is too small to be seen through the fat, but the principal caecal artery in the dorsal fold is visible in part of its course.

*Mystax imperator* has a relatively longer caecum with its apex upturned as in *Hapale*, otherwise it resembles that of *M. midas* in shape. The ileum joins the colon at an angle and across the ileo-caecal angle the ileum is bound down by a continuous, short, thick fold, the rest of the caecum being free. Caecal vessels are entirely sinistral. There is a large, ventral (dextral) lymph gland on the ileo-colic junction.

In *Hapale jacchus* (Pl. III, fig. 14) the colon describes the same general course as in *Mystax*, but the ileum enters it at right angles. The gut is, however, sacculated and provided with two distinct taeniae coli, these being produced proximally onto the basal portion of the caecum.

As reported by Beattie (1927), the caecum is longer than the "ascending" colon and tends to be hooked at its apex. The upturned portion is sharply demarcated from the rest by a constriction and is thicker-walled than the basal portion, and further differs in having a complete longitudinal muscular coat instead of taeniae and haustra. The taeniae fan out gradually from above the mid-point of the caecum to form a complete investment on the terminal upturned segment.

Representatives of all three mesotymphla occur, but not so regularly and symmetrically as in *Mystax*. The short, triangular, anangious, intermediate fold is joined distally by the sinistral fat-laden fold which, as in *Mystax*, descends from the enteric mesentery across the back of the ileum onto the caecum, and carries the long dorsal caecal vessels which proceed to the caecal apex and supply the major part of the viscus. The dextral fold is reduced to a fat-laden plica carrying a fair-sized vessel that supplies the proximal one-third of the ventral aspect of the basal moiety of the caecum—a proportionately greater distributional field than in lemurs.

One specimen of *H. jacchus* had a peculiar arrangement where the two lateral folds flanked a triplicated intermediate mesotymphon, giving five folds in all. The middle element was shortest, quite transparent and anangious; on each side of it was a slightly more extensive fold carrying a thin strip of adipose tissue in its free edge, the rest being filmy and transparent and apparently without vessels. This is undoubtedly an individual variation. Beattie's assessment of the peritoneal relations of the caecum of *Hapale* fits none of the specimens examined by us.

*Hapale argentatus* lacks the upturned apex to its caecum, otherwise it resembles *H. jacchus*. The three mesotymphla are present, but all excessively short, the dextral reduced to a mere ridge with very small vessels, if any, the median anangious and the left with plenty of fat and carrying the principal caecal vessels.

*Hapale santaremensis* (Pl. IV, fig. 15), two specimens examined. In this species



the colon is smooth, without taeniae or haustra. The caecum is longer and more capacious than in *H. jacchus*, but unlike *H. argentatus* carries the upturned globular moiety, giving the organ a general hook-like appearance. The basal portion is vaguely sacculated. The ileum enters at an angle directed cranially. Three mesotyphla occur, the sinistral and dextral both being short and passing but a short distance along the caecum and each carrying a fair-sized vascular trunk. The intermediate fold is more extensive in all directions and its ileal attachment not quite median but somewhat sinistral. It is, however, quite independent of the sinistral vascular fold. A large lymph gland occurs at the base of the dextral fold at the point where it leaves the enteric mesentery to cross the ileo-colic angle. In one specimen (♀), an additional vessel-bearing dextral fold, distal to the typical dextral fold, which carries the ileo-caecal lymph gland, is present. In this case the vessel in the distal fold crosses the terminal part of the ileum to gain its fold. There is, as a result, a deep pouch between the distal dextral and the intermediate mesotyphla.

*Hapale albicollis*.—We have not seen this species, but Klaatsch records the condition of the colon, etc. in two foetal specimens, and his remarks have been much commented upon by later writers (notably by Treves, 1885; Le Gros Clark, 1934; Reider and Straus). Klaatsch noted that in these specimens a rudimentary ansa coli is present, which in the adult has disappeared. He suggested this was a retention of an ancestral lemuroid phase. Recent authors have uniformly condemned this view and as Straus says: "it is extremely unlikely that any phylogenetic significance should be attached to these loops or bends" produced as they are by phases of differential growth in different segments of the large intestine.

*Leontocebus leoninus* has the usual U-shaped form of colon with a wide caecum and "ascending" colon narrowing towards the bend of the U. The caecum is long and bent to the left in hook-fashion, but there was, in our specimen, no sharp demarcation between the recurved portion and the body of the viscus, nor were taeniae detectable. The apex is blunt.

The caecum is provided with three mesotyphla as in *Mystax*, but the dextral and sinistral folds are both low, symmetrically disposed about the much more extensive intermediate fold which passes almost the whole distance along the medial border of the caecum remaining anangious throughout. Vessels proceed within both sinistral and dextral folds, that in the former being the larger; after gaining the periphery of the fold both vessels proceed subserously on the caecal wall. There is a large ileo-colic lymph gland of angular outline overshadowing the ileo-colic junction ventrally and two rounded glands dorsally, the distal one of which lies between the layers of the root of the sinistral mesotyphlon.

*Oedipomidas geoffroyi* (Pl. IV, fig. 15a) likewise presents the U-shaped colon, with long, lateral and short, transverse limbs. The "ascending" portion presents three ill-defined taeniae with intervening feebly indicated haustra. The taeniae fade at the hepatic flexure and also on the caecum. The ileum enters almost at right angles. The caecum was greatly dilated compared with the colon in our specimen, having the form of a short, curved sausage, with blunt, rounded tip directed to the left, but not upturned. It is connected to the ileum by a triangular anangious mesotyphlon. Dextral and sinistral caecal vessels proceed across the terminal

ileum in low fatty plicae, the former being larger than usual, nevertheless, not traceable beyond the mid-point of the caecum. The sinistral vessel proceeds independently of the intermediate mesotyphlon, though close to its attachment to the lesser curve of the caecum ; it proceeds to the apex caeci.

## 2. CEBIDAE.

We have examined the following species of this family :—

*Aotes zonalis* (2 specimens), *Saimiri sciurea* (5 specimens), *Pithecia monachus* (2 specimens), *Cebus xanthosternus* (2 specimens, one new-born and one adult), *Alouatta seniculus* (2 specimens), *Lagothrix humboldti* (2 specimens). *Callicebus* has been reported on by Weldon (1884) and in detail in an important contribution by Johnston (1920), whilst Huntington (1903) has short notes and figures of *Ateles ater*, *Alouatta*, *Lagothrix humboldti* and *Pithecia satanas*.

*Saimiri* (Pl. IV, fig. 16) shows the least advanced condition of the colon and caecum in the whole family, being indeed more primitive than any of the Hapalidae and in fact no more advanced than *Tupaia* or *Tarsius* (see Pl. I, figs. 1 and 2). The large intestine is a short, straight tube, not strictly divisible into colon and rectum. The ileo-caecal junction is at the anterior end of this tube near the median line and caudal to the mesogastric viscera. The mesentery of the large intestine is directly continuous with that of the small bowel and has a simple, straight attachment to the dorsal body wall a little to the left of the median line. The caecum is of only moderate length, narrow near its colic attachment, more dilated distally, with a globular end sometimes hooked (*cf.* Martin, 1833 *b*). It is smooth-walled, without taeniae or haustra and directed cranially. The small intestine enters at an angle to the caecum, but is more in line with the commencement of the colon, with which it agrees in calibre. Across the angle between the ileum and the right border of the caecum stretches a simple median mesotyphlon containing vessels and lymph glands. One gland is placed at the junction of the globular termination of the caecum with the rest of the organ ; another lies on the dextral side of the membrane. A whole row of glands follows the course of the anterior mesenteric artery as it approaches the ileo-caecal junction. At the junction this vessel breaks into two terminal caecal branches, dextral and sinistral. The latter is the larger and is carried in a short, thick plica vasculosa past the gut into the mesotyphlon, where it supplies branches to the caecum as far as its apex. The dextral vessel is also carried in a plica vasculosa. It fails to reach the caecum, terminating on the main gut by dividing into two, a smaller branch to the ileum and a larger to the proximal part of the colon. In consequence of the above arrangement there are no ileo-caecal peritoneal recesses.

*Cebus* (Pl. IV, fig. 17) and *Aotes* (Pl. IV, fig. 18) are more advanced than *Saimiri* in the arrangement of the large intestine, but still fall behind the Hapalidae and the remaining genera of Cebidae. In both these genera the colon takes the form of a narrow inverted U, with short "ascending" and transverse limbs and a longer "descending" limb continued caudally into the rectum. The caecum is relatively short and in line with the ascending colon, but at its apex it changes direction, gradually in *Cebus* but abruptly in *Aotes*. The small intestine, in adults at least,



enters at an angle, but in a new-born *Cebus xanthosternos* we found the ileum more in line with the colon and the caecum springing from the junction at an angle, as in some lower Primates.

The proximal (ascending) colon in *Cebus* is wider than the rest, and is also wider than the caecum. In *Aotes*, as found in *A. azarae* by van Loghem, both caecum and proximal colon are greatly increased in calibre as compared with the rest, giving this part of the gut the appearance of an accessory stomach. *Aotes* is unique in the family in the nature of its upturned terminal segment of the caecum which can, with some justification, be referred to as an appendix, for it is considerably constricted compared with the sac-like basal portion, besides being thicker walled. *Aotes* agrees with *Callicebus personatus*, in three specimens of which Johnston (1920) observed a well-marked caeco-colic valve was present with a central opening, attached above the ileo-caecal valve. It is marked by an annular constriction externally. Several incomplete constrictions also occur on the body of the caecum in *Aotes*, giving a pseudo-sacculated appearance.

As regards mesotyphla, *Cebus* is more typical than *Aotes*. In the former genus dextral and intermediate mesotyphla of equal extent are present. The sinistral fold is represented by a plica vasculosa only, the dorsal caecal vessels crossing the ileum subserously to gain the intermediate fold as in *Lemur*. A relatively large number of vessels are transported in the dextral fold supplying the area opposite the entrance of the ileum and adjacent areas of colon and caecum.

*Aotes* lacks the intermediate mesotyphlon. The caecum receives its vessels from low, thick dextral and sinistral folds, each containing considerable fat around the vessels. In one of our specimens the caecum is supplied principally from the vessel in the dextral fold; in the other the sinistral fold carries the main supply. Whether the arrangement is indiscriminate or whether, indeed, 50 per cent. are supplied from the dextral and the rest from the sinistral vessel, cannot be stated without further material, but the presence of a large number of vessels derived from the dextral fold in some examples of *Cebus* is suggestive. The question is of some importance in connection with the aberrant arrangements sometimes occurring in *Homo* (*vide infra*, p. 231). In the case where the sinistral vessel was the smaller it supplied an area of the base of the caecum on its dorsal side only.

*Callicebus*, according to the researches of Weldon (1884) and Johnston (1920), aligns itself close to *Aotes* in the characters of its alimentary canal. Weldon, who examined *C. gigot* and *C. moloch*, found the caecum to be separated from the colon by a permanent constriction, and the caecum to be of moderate length, gently curved and with a rounded, blunt apex. The basal portion, of greater calibre than the rest, was found to taper gradually into the narrower apical segment in *C. gigot*, but to be separated by an abrupt constriction in *C. moloch*, where the terminal segment resembles a vermiform appendix, presumably like that of our specimens of *Aotes*. Johnston, who examined *C. personatus*, found a caecum of similar proportions and shape, but the terminal narrowed segment was bent in the form of a hook, which in some individuals is prolonged into a spiral coil (*vide*, Pl. IV, fig. 18a). Clearly, in this genus, animals dying in different phases of bowel contraction can, like some Catarrhine genera, produce at any rate a temporary appearance resembling a vermiform appendix whether or not this portion of the gut is physiologically

differentiated from the remainder of the caecum. Johnston further notes an elaborate caeco-colic sphincter in this genus and points out the presence of the "anterior" and "posterior" vascular folds of Huntington, but makes no mention of the intermediate fold. In two of his three specimens the sinistral vessel was the larger and extended to the apex of the caecum. The third example presumably had the dextral vessel carrying out the larger duty as in one of our *Aotes*.

The genera *Pithecia*, *Alouatta*, *Lagothrix* and *Ateles* comprise a group, as far as their alimentary systems are concerned, much more advanced than any of the Cebidae so far dealt with, approaching, indeed, the state observed in the Catarrhini.

In *Pithecia monachus* the colon describes a simple inverted U-shaped curve, broader than in *Cebus*, but narrower and with longer lateral limbs than in *Alouatta*. It is smooth-walled, i.e. without taeniae or sacculations. It commences at a well-marked caeco-colic constriction which is about an inch beyond the right-angled entrance of the ileum (*vide*, Pl. V, fig. 19). The "ascending" colon has a broad base immediately beyond the constriction, but narrows to a uniform calibre, which is retained until the rectum is reached.

The caecum is long and capacious. Broad in calibre at the ileo-caecal junction, it narrows very gently towards its upturned blunt apex. Its left border is connected to the ileum by an extensive vessel-bearing mesotyphlon, which appears to consist fundamentally of the originally anangious fold that has received the sinistral caecal vessels secondarily from a plica vasculosa crossing the terminal ileum. These vessels supply the distal two-thirds of the caecum and the dorsal aspect only of its proximal third. Two vessels are also given off to the antimesenteric border of the ileum, the distal one very slender and running in the free edge of the mesotyphlon. A dextral (ventral) caecal artery, like its partner, accompanied by lymph glands crosses the ileo-caecal junction in a slightly raised fold. It is distributed to the ventral aspect only of the proximal third of the caecum by a leash of five branches and there is no anastomosis with the other system.

The caecum of the related genus *Cacajao* has been considered by Forbes (1880) and Mitchell (1905), both of whom studied *C. rubicundus*. Forbes' account is by far the better of the two. He states that the caecum is of larger calibre than the colon and cylindrical in shape, unsacculated, curved and blunt-tipped. The curvature is such that when distended the organ described more than a circle. A well-marked median mesotyphlon is present. Mitchell merely describes the caecum as "single", capacious, tapering to a point and slightly twisted spirally.

*Alouatta seniculus* (Pl. V, fig. 20) (two examples examined) retains the simple U-shaped colon, but the U is broad with short limbs as in *Pithecia*. It is of considerable calibre throughout, with consequently a relatively short mesocolon. It is smooth-walled and unsacculated (Flower, 1872, described a single taenia). The ileum enters at an angle, being directed cranially and to the right. The caecum is shortish, but very capacious. Its proximal part is in line with the colon and similar to it in calibre, but distally it curves to the left and dilates, to end in a blunt, rounded terminus. Its left border is connected to the ileum by an extensive median anangious mesotyphlon. Additional dextral and sinistral folds are present, both bearing vessels and lymph glands. The principal vessel is the dorsal (sinistral) one.



Huntington describes a similar arrangement in *A. ursina* (= *Mycetes fuscus*), where the sinistral and dextral vessels are of equal size and both shorter than the median fold.

There is no caeco-colic constriction in this genus.

*Lagothrix humboldti* (Pl. V, fig. 21) has made a further advance. Its colon is much longer relatively than in all the Cebidae so far considered, being arranged as in Man, with definite hepatic and splenic flexures but retaining its mesenteries throughout as in Catarrhini. We find all sections of the tube equally sacculated, but the sacculations are principally observed on the antimesenteric wall of the gut. Bradley (1903), who described the abdominal viscera of *Lagothrix* in great detail, found the sacculations fainter on the transverse than the "ascending" or "descending" colons. Taeniae are present, though indistinct, three in number on the "ascending" colon, one lateral, one dorsal and one ventral. The lateral band, according to Bradley, is the most distinct, and is traceable for the greatest distance aborally.

The caecum is in line with the "ascending" colon and equal to it or slightly larger in calibre. It takes the form of a bent tube, the distal third or rather more being sharply upturned and fixed in this position by its peritoneal connections to the neighbouring segments of gut. In contrast to the colon, the caecum is unsacculated and lacks taeniae.

As regards mesenteries, we find a well-defined intermediate mesotyphlon and a shorter dextral fold, but the sinistral fold poorly represented. Bradley, though admitting that the two sections of caecum "are bound together by the peritoneum passing from one to the other", states that there is no "attempt at the formation of a mesocaecum", which seems contradictory.

Vascular arrangements are, in the specimens we studied, the reverse of what is general for the Primates and agree with one of our specimens of *Aotes*, viz. that the principal artery to the caecum is the dextral (or ventral caecal) vessel, which is in line with the main anterior mesenteric, crosses the terminal segment of the ileum some distance proximal to the ileo-caecal junction and enters the dextral mesotyphlon, where it divides into a smaller proximal and a larger distal branch. The former supplies the basal part of the caecum on its ventral face, whilst the latter ramifies on the rest of the caecum, except for the small area on the dorsal aspect, which is supplied by the small sinistral vessel. The ventral caecal vessel is related in the dextral fold to a lymphatic gland. Other glands exist in the enteric mesentery at the ileo-colic angle. The above arrangement confirms that observed by Huntington in *Lagothrix*.

*Ateles*, according to descriptions in the literature (we have seen no specimen ourselves), possesses the most advanced form of large intestine among the Platyrrhini, approaching closely conditions observed in Catarrhini. Mitchell (1905) states that the ileum passes into the junction of caecum and colon at a relatively acute angle "and in such fashion as to suggest the vestigial presence of a second caecum". The caecum is relatively short and forms an elongated, pointed cone which may be slightly coiled. This closely simulates the organ in Catarrhini. Huntington states that in *A. ater* there is a caeco-colic constriction. Van Loghem refers to three wide taeniae commencing about half-way along the caecum and

continuing aborally on the "ascending" colon, where they narrow down; only the ventral band remains distinct on the transverse and "descending" colons, the others fading gradually. Haustra are recognizable throughout the colon.

The caecum in *Ateles ater* is described and figured by Huntington as being connected to the ileum by a short, anangious median mesotyphlon, flanked by longer vessel-bearing membranes that descend across the ileum dorsally and ventrally from the corresponding aspects of the enteric mesentery. Both dextral and sinistral vessels are shown of the same approximate size, both passing to the caecal apex. If this is true the condition is unique and needs further investigation.

A similar condition was described and figured by Treves, whose account leads to the assumption that dextral and sinistral vessels, like their associated folds, are of similar size. Treves' figure shows the large dextral vessel proceeding as far as the tip of the caecum—the same as we have noted in *Lagothrix*, but in *Ateles* this does not appear to be a substitution for a degenerated sinistral trunk.

### IX. CATARRHINI CYNOMORPHA.

In the general disposition and structure of the large intestine and its appendages the Cynomorph Catarrhines exhibit a striking uniformity, wherein they contrast strongly with the Platyrrhini, on the one hand, and the Anthropomorphs, on the other. They are, as already has been noted, however, closely approached among the Platyrrhini by *Lagothrix* and *Ateles*.

A general description of the Cynomorph colon and caecum will suffice, followed by short notes on the principal genera, most of which we have, ourselves, examined.

The colon is arranged fundamentally in the same fashion as in Man and has a general similarity in appearance to the human colon, since it presents typically three taeniae and is sacculated throughout. It differs in its greater relative length and mobility, being thrown into coils, especially in its "descending" portion and possessing a continuous mesocolon. Hepatic and splenic flexures are well marked. The colon considerably exceeds the small intestine in calibre.

The caecum is of similar calibre to the colon but is short and subglobular in outline. It tends, however, to be differentiated into two regions:—(i) a basal, more globular region, possessing taeniae and sacculations, the former continued from the "ascending" colon; and (ii) an apical region of variable shape, thicker-walled and with a complete longitudinal muscular coat produced by the expansion and fusion of the three taeniae.

This apical segment varies in shape, not only individually but in the same individual at different times, due to the state of contraction or relaxation of the muscular coat. We have observed, for example, in *Cercopithecus aethiops sabaeus* that a caecum presenting to all intents and purposes a sharply demarcated vermiform appendix (like that figured in *C. ascanius* by Neuville, 1922 and *C. aethiops tantalus* by Wood-Jones, 1929\*), when the muscular coat is contracted, changes

\* *Macaca*, at least, seems to share these occasional vermiform terminations of its caecum with *Cercopithecus*, for Hervé (1882), in an undetermined species, Keith (1891), in *M. nemestrina*, Weinberg (1906), in *M. irus* and *M. sinica* and Neuville (1922), in *M. irus*, *M. sinica* and *M. mulatta*, have reported their occurrence. Keith, moreover, notes having observed it in a Leaf-monkey, which is less understandable in view of our findings in this group (*vide infra*).



into one with a broad-based conical apex when distended by preservative fluid after removal from the body. Soon after death, whilst the musculature is still contractile, these changes can be observed taking place. The sacculations of the basal portion of the caecum may be asymmetrical, so that the conical region may then be directed towards the mid-line or even cranialwards, since the lateral sacculations tend to exceed the medial in size.

The caecum is invariably connected to the antimesenteric border of the ileum by an extensive triangular sheet of peritoneum (intermediate mesotyphlon) and this is generally anangious. Dorsal and ventral caecal arteries occur, both derived from the anterior mesenteric. The former is invariably the larger and supplies the apical portion of the caecum and at least the dorsal aspect of its basal segment. The ventral vessel is limited in its distribution, supplying, at most, the ventral aspect of the basal segment. These vessels gain the caecal wall by crossing the terminal portion of the ileum in fat-laden peritoneal folds of varying development, often containing lymphatic glands in addition. The dorsal (*i.e.* sinistral) fold frequently fuses with the intermediate mesotyphlon and delivers its vessels thereto, before gaining the caecal wall.

Occasionally the intermediate mesotyphlon is fatty, in which event dissection reveals the presence of a vessel coursing from the distal border towards the ileo-caecal angle; it is a recurrent branch from the sinistral caecal artery.

#### 1. CERCOPITHECIDAE.

##### *Macaca.*

We have examined examples of *M. mulatta*, *M. irus*, *M. nemestrina*, *M. cyclopsis* and *M. sinica*. In advanced foetuses and new-borns, at least of *M. mulatta* and *M. sinica*, there is no "ascending" colon, but the ileo-caecal junction lies cranially against the posterior aspect of the liver, the caecum being directed caudalwards or even slightly to the right and the terminal ileum being directed cranially and to the right. The caecum, at this stage, is a simple, symmetrical cone, but sacculations are evident on its basal portion.

In adults the caecum has migrated caudally to permit the formation of an "ascending" colon. It is short, blunt and sacculated only at its base. The apex may be rounded or roundly pointed and with a complete longitudinal muscular coat, in contrast to the basal segmented portion with its three taeniae. The ileum joins at a fairly acute angle and its antimesenteric wall is connected to the left wall of the caecum by a triangular anangious intermediate mesotyphlon. Dorsal and ventral caecal vessels proceed across the terminal ileum in plicae vasculosae, the former containing a large lymph gland. In *M. nemestrina* these plicae do not obscure the ileo-caecal angle, but in *M. mulatta* we find the dextral fold at least is raised to form a definite dextral ileo-caecal recess; the sinistral fold is less extensive but, like the dextral fold, contains lymph glands.

In the adult *Macaca sinica* the caecum is decidedly asymmetrical, with the apex directed to the left. The apical region is pointed and thicker walled than the larger sacculated basal portion. The intermediate fold extends as far as the apex and tends to be fat-laden. In one adult male we found a vessel passing into this after crossing the ventral wall of the ileum subserously about an inch proximally (orally) to the ileo-caecal junction.

We have examined specially the Formosan Macaque (*M. cyclopsis*) in view of Neuville's expectations regarding dietary effects on caecal structure. This author spent much labour detailing the dietary variations of different Primate genera and species in an endeavour to evoke evidence of their bearing on caecal anatomy. He cites the present species as differing from other Macaques in its habits and diet, subsisting entirely on such fodder as is to be obtained in a dry, rocky, treeless terrain, namely dry, coarse grasses and woody fibres, roots, etc. We find, however, no differences in the caecum of this animal from that of other Macaques. Our specimen has a fairly symmetrical caecum, in line with the colon, and with a conical apical segment upon which the taeniae spread fanwise rather than abruptly. The median mesotyphlon is extensive and proceeds to the caecal apex.

#### *Cercocebus.*

In several examples of *C. atys* we find the details as described by Bradley (1903), who considered this species under the name *C. fuliginosus*. The colon is arranged as in *Macaca* and is similarly provided with three taeniae and distinct haustra. The caecum is short but capacious, curved to the left and with a blunt, rounded apex which is not appreciably thickened like that of *Papio* or *Macaca*. A thin, extensive, triangular, anangious mesotyphlon connects the lesser curvature of the caecum with the antimesenteric aspect of the ileum. Both dextral and sinistral vessel-bearing, fat-laden folds are present, both outstanding as sharp ridges and both carrying lymph glands.

In *Cercocebus atterimus* we find the caecum to resemble rather that of the Colobidae than the other members of its own group, the organ being short, relatively globular in shape and with the taeniae spreading rather sooner to give a uniform longitudinal muscular coat over almost the distal half of the sac. The rounded apex has a thicker wall than the rest. The caecum is in line with the colon, and forms a single sac without parietal sulci, but it is not constricted at its neck like that of the Colobidae. The intermediate mesotyphlon is the only extensive fold present and in our specimen is avascular. The sinistral vessel proceeds subserously near the caecal attachment of the above-mentioned fold and is accompanied by a lymph gland. The dextral vessel bifurcates into a branch for the region opposite the ileal entrance and another to the ventral wall of the caecum medial to the ventral taeniae.

#### *Baboons.*

The Baboons of the genera *Papio* and *Mandrillus* possess a more asymmetrical and more fully differentiated caecum than the preceding Cynomorpha. We have examined examples of *P. papio* (3 specimens), *P. anubis*, *P. hamadryas* (one each), and *M. leucophaeus* (3 examples). In juveniles the caecum is relatively symmetrical, being a short, cylindrical tube with bluntly-rounded apex. With advancing age, the organ becomes more and more asymmetrical through the considerably greater growth of its morphologically distal (*i.e.* topographically right) wall, whereby a J-shaped structure (as judged by the direction of the taeniae) is produced—with the short limb of the J turned to the left. The upturned portion is the morphological caecal apex and is bulbous, thick-walled and sharply demarcated from the rest of the viscus, which is strongly sacculated (*vide*, Pl. V, fig. 22).



In *Mandrillus* a more primitive condition is retained, with the apex very broad and rounded and not markedly upturned, the whole organ being very capacious. In all the above the arrangement of the mesotyphlon and adjacent folds is the same as in *Macaca* and *Cercocebus*. The dextral fold is feeble, but commences high up on the enteric mesentery; it contains fat and lymph glands as well as vessels. The sinistral fold may not be raised appreciably unless fat-laden, in which case the posterior caecal vessels cross the ileum subserously to gain the caecum. Both sets of vessels are distributed on the caecum subserously, leaving the median mesotyphla completely anangious.

In one example of *P. papio*, an adult female, the mesotyphlon was not anangious, but carried a recurrent vessel from the dorsal caecal artery as it coursed towards the apex caeci. This vessel also contributed a well-marked branch to the ventral aspect of the apical area of the caecum, the dextral vessel being responsible for the supply of the basal region only of the ventral caecal wall.

The caecum of the Gelada (*Theropithecus gelada*) was mentioned by Garrod (1879) as sacculated and as lacking an appendix. Details doubtless differ little from those of the preceding Cynomorpha.

#### *Erythrocebus.*

In *Erythrocebus patas* we find a shortish, subcylindrical conical-tipped caecum with only two distinct taeniae, the third (medial) being indistinct and obscured by the attachment of the median mesotyphlon. The organ is almost symmetrical, its axis continuing the general curve of the "ascending" colon. The main part of the caecum is distinctly sacculated, but the conical termination is smooth-walled, due to the expansion of the taeniae to give a complete muscular coat. The ileum joins at an acute angle, which is bridged by the triangular median mesotyphlon. This receives vessels dorsally from a sinistral plica vasculosa; the advent of the vessels producing a distinct traction of the mesotyphlon dorsalwards and also causing the formation of a shallow pouch. These dorsal caecal vessels proceed distally very close to the caecum, leaving the major part of the mesotyphlon quite anangious. The condition, however, is, in this respect, an advance on the completely anangious state observed, e.g. in *Macaca* and *Papio*. A few small, ventral caecal vessels cross the ileo-caecal junction in a short, broad peritoneal fold, which also supports a large-lymph gland.

#### *Cercopithecus.*

Of the genus *Cercopithecus*, we have examined several specimens of the common Green Monkey (*C. aethiops sabaeus*), two of *C. albigularis kolbi* and one each of *C. mona campbelli* and *C. diana*. All agree in the essential particulars of the caecum, which, in shape, more closely resembles that of *Papio* than that of *Erythrocebus*. It is asymmetrically curved, so that its apex points to the left. The roundly-pointed apex is markedly distinct from the basal sacculated region, there being a deep constriction between the two. The sacculated portion displays three distinct taeniae; these approach and fuse abruptly at the junction with the apical, thick-walled region.

The mesotyphla are relatively primitive, comprising an extensive membranous

median anangious fold, flanked by two equally developed fatty vessel-bearing folds separated by peritoneal fossae from the median fold. The fatty folds cross the surface of the terminal ileum from an origin on the enteric mesentery. The dextral one frequently shows a transverse fatty lobe accompanying a branch of the ventral caecal artery that supplies the ventral wall of the gut opposite the ileo-caecal junction.

## 2. COLOBIDAE.

Despite the differences in the upper alimentary tract between members of this family and those of the Cercopithecidae, the general features of the ileo-caecal region are very similar, though significant differences in detail occur.

We have examined *Semnopithecus priam* (one foetus, one new-born), *Kasi senex* (= *S. cephalopterus* of earlier authors; 7 specimens), *Presbytis femoralis chrysomelas* (one juvenile), *Colobus abyssinicus matschiei* (two adults) and *C. a. abyssinicus* (one adult).

The colon is disposed as in the Cercopithecidae and is fully sacculated, provided with taeniae and very capacious. Due to the enormous size and specialization of the stomach and the consequent displacement of the liver, there is scarcely any "ascending" colon, even in the adult. There is, however, a very distinct hepatic flexure about one inch anterior to the ileo-caecal junction. Across it the colic attachment of the great omentum is drawn as far as the ventral taeniae, to which this fold is connected.

The caecum in all the species examined depends from the ileo-colic junction as an unsacculated, egg-shaped sac with a slightly constricted neck, broad across its middle and narrowing to a blunt fundus posteriorly. There is no constricted or thickened terminal portion. We cannot agree with Mitchell's (1905) estimate of the caecum of Semnopithecinae as "conical". Morphologically the major part of this peculiar caecum corresponds to the thickened, unsacculated apex of the caecum of *Papio* and its allies. This is indicated by the behaviour of the taeniae, which commence to fan out immediately beyond the ileo-colic junction and have fused, to give a complete muscular investment to the caecum, at about its middle in *Kasi* and even earlier in *Colobus* (*vide* Pl. VI, figs. 23 and 24).

The caecum is connected to the ileum by a broad membrane representing the intermediate mesotyphlon. There are no true dextral or sinistral mesotyphla, these being represented at most by ill-defined plicae vasculosae, the sinistral, carrying the principal caecal vessels, being the better indicated. In *Kasi senex* the ventral artery is represented merely by an anastomotic loop coursing across the termination of the ileum subserously to unite in the ileo-caecal angle with the dorsal vessel. The dorsal artery proceeds peripherally subserously or in the caecal attachment of the intermediate fold; but in *Colobus*, at least, although mainly running wholly sinistral to the caecal attachment of the mesotyphlon, yet it contributes thereto a recurrent branch which breaks up into twigs supplying the anti-mesenteric wall of the terminal ileum (Pl. VI, fig. 24 b).

In the foetus of *Semnopithecus* the colon preserves a primitive arrangement, recalling that of *Saimiri*; thus the ileo-colic junction lies in contact with the liver and the transverse colon is short and soon succeeded by a long, coiled "descending" colon. The caecum is relatively longer than in the adult, cylindrical in form, but



with the apex, comprised by its terminal third, thickened and sharply reflected on itself and adpressed to the basal portion. The intermediate membranous mesotyphlon is present and extends to the upturned apex; no flanking vessel-bearing folds are developed. The apical thickening is lost after birth as the gut becomes functional and does not appear to be temporarily reassumed during phases of muscular contraction as it is, for instance, in *Cercopithecus*.

In the early post-natal stage, the adult disposition of the parts has already been attained.

In view of Keith's (1891) findings on the Siamese Leaf-monkey, termed by him *Semnopithecus albocinereus* and now known as *Presbytis femoralis siamensis*, where he observed its caecum "sometimes resembles that of the pig-tailed baboon" in having a terminal contracted region, we have made a special point of examining a young individual of the Bornean race (*P. f. chrysomelas*) of the same species. In this we find little difference from the caecum of *Semnopithecus priam* of corresponding age. Caecum and "ascending" colon are of equal calibre, exceeding that of the remainder of the colon. The caecum is L-shaped, the vertical limb in line with the colon, the transverse limb directed to the left and narrowing to a roundly-pointed apex instead of being recurved sharply as in the young *Semnopithecus*. Sacculations are present on the colon but lacking from the caecum. The median mesotyphlon is of considerable extent and receives dorsally the large posterior caecal vessel which supplies a large branch to the ileum in addition to its caecal distribution. No dextral fold is present.

#### X. HOMINOIDEA (ANTHROPOMORPHA + HOMINIDAE).

The Anthropoid Apes and Man agree in the essential features of the caecum and are usually regarded, with some justification, as standing well apart from the lower Primates in that respect. The main differences seem to be the adaptations to the orthograde posture and involve more or less shortening of the colon and its partial fixation to the body wall, further reduction of the caecum and sharp demarcation of the caecum proper from its terminal thickened moiety that takes on the form of a definite, elongated vermiform appendix. Although all the genera agree, their importance demands individual consideration.

##### 1. HYLOBATIDAE.

This group has been previously dealt with by Owen (1868), Broca (1869), Kohlbrugge (1891), Klaatsch (1892), Chapman (1900), Huntington (1903), van Loghem (1903), Mitchell (1905) and Wood-Jones (1929). We have examined specimens of *Hylobates concolor leucogenys*, *H. cinereus abbotti*, *H. lar agilis* (2 specimens), *H. l. lar* and *H. hoolock*.

We find the caecum and ascending colon to be quite free from the dorsal abdominal wall. In *Symphalangus syndactylus*, according to van Loghem, the upper part only of the ascending colon is fixed. Fixation appears to take place first, therefore, in the neighbourhood of the hepatic flexure. The ascending colon is developed early, as we find it already of some length in a juvenile *H. cinereus abbotti* (Pl. VI, fig. 25). Both Kohlbrugge and van Loghem report four taeniae coli. We find a ventral one, two posterior ones and a meso-colic (*i.e.* medial) taenia.

The caecum is short, globose and sacculated ; descends directly in line with the ascending colon and is reasonably symmetrical (*cf.* Owen), for the appendix arises from its most dependent wall, though overshadowed in adults by the caecal haustra, thus confirming the observations of Kohlbrugge and Sonntag (1924). In juveniles Treves' foetal form is preserved, the caecum, though quite distinctly sacculated, narrows gradually, merging imperceptibly into the commencement of the appendix. The appendix is long, vermiform and twisted on itself, sometimes with irregular kinks ; at others spirally twisted anti-clockwise. The appendix has its own mesentery (meso-appendix) derived primarily from the sinistral mesotyphlon, which carries the posterior caecal vessels from the dorsal aspect of the enteric mesentery, past the terminal ileum to the caecum and appendix—almost to the apex of the latter. A shorter " bloodless " fold of Treves, morphologically equivalent to the intermediate mesotyphlon of the lower Primates, connects the antimesenteric wall of the terminal ileum with the opposing wall of the caecum, and is separated from the vessel-bearing fold by a pocket of greater or lesser depth. Sometimes, as in our specimen of *H. cinereus*, the bloodless fold loses its independence at its extreme distal limit, where it fuses with the sinistral fold just before gaining the caecum. The same was found in our *H. concolor*. A short, thick dextral fold, often laden with lobules of fat, crosses the front of the ileo-colic junction and transmits short anterior caecal vessels to the front of the caecum proper. This fold also supports a lymph gland, but the fold is not sufficiently free to form any anterior or " superior " (Waldeyer, Treves) ileo-caecal fossa (ileo-colic of Berry).

*Hylobates hoolock*, on the contrary, is more primitive, for it possesses a long, independent, completely anangious intermediate mesotyphlon flanked by dextral and sinistral folds.

## 2. PONGIDAE.

In all the great apes, as in *Homo*, the ascending colon becomes fixed on the dorsal body wall, but the transverse colon retains its mesentery. Three taeniae are invariably present throughout the colonic length, which is also distinguished by the possession of appendices epiploicae. Varying arrangements in the forms of loops have been described on the colon. These appear to be mainly individual variants. We have noted a U-shaped dependent loop on the transverse colon of a young Orang, in which a plica was pulled down from the great omentum towards the apex of the loop. We do not consider this to be homologous with the lemurine *ansa coli*. Another unusual arrangement was observed in adult Chimpanzees and Orangs, but this has no bearing on the present problem and warrants publication in a separate contribution.

### *Orang-utan.*

We have examined five Orangs as follows :—

1. Mid-term foetus (C.R. 174 mm.)
  2. Neonatus (5 days old)
  3. Juvenile (several months old ; died in Regent's Park).
  4. Older juvenile (in Royal College of Surgeons).
  5. Adult female (in Anatomical Museum, Edinburgh).
- } in Anatomical Museum, Edinburgh.



In all these the caecum is an asymmetrical organ distinctly different from that of *Hylobates*. Instead of lying in line with the ascending colon it is curved to the left and its morphological apex is directed upwards behind the terminal ileum, due to the formation of a single large sacculaton on its right (parietal or antimesenteric) wall.

In shape the caecum differs from that typical for other Pongidae and Hominidae. It consists of a single, large, irregularly pyriform sacculaton, simulating a stomach in reversed position. Thus it bears an extensive, convex greater curvature directed infero-laterally, and a very short lesser curvature directed upwards and to the left. The two meet in a conical apex whence springs the vermiform appendix. This apex is directed upwards and to the left behind the terminal ileum. We cannot, therefore, agree with Chapman's (1880) estimate that there is no difference between the human caecum and that of the Orang. It applies least of all to juveniles, and Chapman's specimen was a young male! Straus' account is substantially the same as our own, but in his adult male an additional sacculaton is described and figured above the main caecal sac. This is separated by a deep lateral constriction from the caecum proper and is clearly regarded as part of the ascending colon. It is clearly the caecal colon of Keith (1904). The caecal sac in our adult female is also deeply demarcated from the lowest lateral haustrum of the colon, but this colonic sac is not as dilated as in Straus' example.

The taeniae are indistinct and spread out gradually in the youngest specimens, but are more distinct in the older ones. In all, the peritoneum is carried onto the dorsum of the organ, which is thus free, except for a single parieto-colic fold in the older of the three juveniles.

The appendix is long, greatly kinked and arises from the conical morphological caecal apex. The caecum and appendix receive their blood supply in the Orang in the same manner as in Man. The main vessel is the posterior caecal, which is carried from the enteric mesentery in a sinistral fold that becomes the meso-appendix, as in the Gibbon. A short "bloodless" fold of Treves lies anterior to the meso-appendix in the ileo-caecal angle, producing a posterior ileo-caecal fossa of some depth. The two are quite independent and are strikingly different in appearance when the meso-appendix contains fat, which is frequently the case. The intermediate or "bloodless" fold extends as far as the first part of the appendix. The dextral fold is represented in our younger juvenile individual by a thick, fat-laden strand arising from the peritoneum to the left of the commencement of the ascending colon, crossing the ileo-colic junction and terminating on the anterior wall of the caecum. It contains the anterior caecal vessels and a lymph gland. It was lacking from our older juvenile animal. The appendix of this older specimen presented two raised, fat-laden folds coursing along its left wall. One of these was a continuation of the meso-appendix; the other, parallel to it and the same length, but separated by a tract covered only by normal peritoneum, was in line proximally with the "bloodless" fold, though divorced from it. The fat content of this second fold would appear to be deposited from recurrent blood vessels received secondarily from the meso-appendical vessels. The bloodless fold was lacking in our adult female, and the sinistral fold had lost its mesenteric connection, having become fused at its root with the dorsal parietal peritoneum—partaking thus of the general meso-colic

fusion. A deep fossa was formed between the terminal ileum and the root of the meso-appendix. An anterior fossa was also (Pl. VI, fig. 26) well developed between the fatty dextral fold and the small gut.

The neo-natal specimen presented an interesting anomaly in which the anterior caecal artery had usurped the duties of the posterior caecal and appendical arteries, and consequently the meso-appendix was dextral in position. The appendix itself was directed somewhat ventrally, looped on itself and terminated in a slightly bulbous tip over the ventral aspect of the terminal ileum. A bloodless fold lay behind the meso-appendix, separated by a peritoneal fossa; but no sinistral fold was present. These anomalies were not present in the foetus, which was the product of the same parents as the neo-natus. In this the peritoneal folds were normally disposed and the long appendix was directed into the pelvis minor, though otherwise similar in shape to that of its brother.

#### *Chimpanzee.*

The caecum of the Chimpanzee (*Anthropopithecus troglodytes*) (three adults and one juvenile examined) is likewise short and globose. It is scarcely distinguishable from the human organ, being grossly asymmetrical and provided with three distinct taeniae that converge towards the origin of the appendix. It differs from the Orang's caecum in being provided with several sharply-defined sacculations, the greater curvature being deeply indented by as many as six sulci between the level of the ileo-caecal valve and the commencement of the appendix; three similar indentations occur on the lesser curvature. It resembles the Orang's caecum, however, in the fact that the terminal compartment is conical, narrowing gradually to the commencement of the appendix, though an external constriction marks the division between them (*cf.* Owen). We cannot, therefore, agree with Reider that in this species "the infantile form predominates", a statement apparently based upon the observations of Gratiolet and Alix (1866), Flower, van Loghem and Huntington—all doubtless based on juvenile Chimpanzees. A caeco-colic sphincter appeared to be present, situated below the shelf-like ileo-caecal valve. The appendix is long and coiled and springs from the left aspect of the caecum behind the terminal inch of the ileum, which last ascends very obliquely to its termination.

The meso-appendix is formed, as in Man and the other anthropoids, from the sinistral aspect of the mesentery. It carries the appendical artery from the ileo-colic trunk to the appendix, extending as far as the tip of the organ. The "bloodless" fold is present, but represented by a short, thick peritoneal duplicature that shows evidence of becoming reduplicated by an invagination of its free edge. This is suggestive of the manner in which Keith (1904) maintains that the ileo-caecal and ileo-colic fossae are differentiated during human ontogeny. The caecum is supplied by anterior and posterior caecal arteries which are distinct from each other and from the appendical. The anterior vessel crosses the large bowel subserously just above the termination of the ileum, but is usually embedded in fat, which may become lobulated and raise a dextral (ileo-colic of Berry) fold. In the absence of fat, the fold (and consequent fossa) are lacking. The artery supplies the anterior wall of the large gut opposite the ileo-caecal union, but does not transgress the most proximal indentation of the lesser curvature of the caecum. The anterior caecal



wall distal to this indentation is supplied by a branch from the posterior caecal artery proceeding forwards subserously, beneath the termination of the ileum and across the root of the "bloodless" fold. The posterior wall of the caecum is vascularized by four branches derived from the posterior caecal stem, which also supplies colic and ileal branches.

The long appendix is provided with several parallel, raised adipose tracts covered by peritoneum. Some of these are of the same character as appendices epiploicae, which are numerous in the Chimpanzee. Two, however, are more outstanding. One is a continuation of the meso-appendix. The other lies more anteriorly and is connected distally with the preceding. Proximally it appears in line with the bloodless fold, of which it would appear to be a divorced remnant that has acquired vessels at its distal end from those in the sinistral fold. A similar structure has been noted above in the Orang, and has also been observed in the Gorilla (*vide infra*).

A strong parieto-caecal peritoneal fold connects the large gut, opposite the ileo-caecal junction, with the parietal peritoneum. It proceeds onto the bowel as far as the lateral border of the anterior taenia.

#### *Gorilla* (*Gorilla gorilla*).

We have examined an infant male and fortunately also had access to records of two others dissected by Professor A. J. E. Cave, to whom we are greatly indebted. These were an infant male in St. Thomas' Hospital and a sub-adult female ("Moina"), formerly living in the Society's gardens and now preserved in the Royal College of Surgeons.

The caecum is in form more like the human organ than is that of the Chimpanzee, the appendix being more sharply demarcated, instead of attached to a funnel-shaped prolongation of the caecum. It must be noted, however, that Deniker (1884) found a gradual transition in the foetal Gorilla. The sulci intervening between the sacculations are less numerous than in the Chimpanzee and, in the juveniles, are incomplete and remarkably shallow, except for the most distal one, which, at the fundus, divides the lateral from the medial sacculatation. The last-named incisure is remarkably deep in our specimen, whilst a second, situated still more medially and dividing the medial sacculatation from another to which the appendix is attached, is also deep, though otherwise not extensive. A transverse sulcus crosses the caecum at its junction with the colon at the level of the upper border of the ileo-caecal valve. It marks the site of a caeco-colic sphincter which, internally, forms a diaphragm with a comparatively small central opening. The medial part of this diaphragm is derived from the superior lip of the ileo-caecal valve. A short, triangular "bloodless" fold connects the antimesenteric wall of the ileum with the lesser curvature of the caecum. It is separated by a deep fossa from the meso-appendix, which descends behind the ileum from the dorsal aspect of the mesentery. In the infant a retro-ileal fossa, like that we have noted in the Orang, separates the last few millimetres of the ileum from the root of the meso-appendix. A fat-laden dextral fold, carrying the anterior caecal artery, crosses the front of the ileo-caecal junction, descending some distance on the caecum. It has attached and distinct free edges, the latter forming the boundary of the

"ileo-colic" fossa. The distribution of the vessels appears to be identical with that described above for the Chimpanzee.

Along the appendix, in the older Gorilla, are two fat-laden tracts, one continuous with the meso-appendix, the other placed more anteriorly and in line with the "bloodless" fold, a feature already noted in both Orang and Chimpanzee.

#### *Homo.*

The human caecum and its appendages are now so well known, resulting especially from the researches of Treves (1885) and Berry (1897), that a full description is not called for. These authors, however, had not the advantage of so large a comparative series of subhuman Primates as we have ourselves had the fortune to examine; they therefore missed certain points that appear to us to be of some morphological value.

The human caecum varies in shape with age and also individually. Treves' four types are well recognized, the infantile (Treves' second) type, resembling the adult organ of *Hylobates*, persisting in 3 per cent. human adults. Treves' third type is the normal adult condition, with the distal saccules asymmetrical in size, due to the greater rapidity of growth of the lateral saccule, and consequent diversion of the morphological apex to the left. The fourth type, an exaggeration of the normal, is formed by greater growth of the lateral saccule accompanied by atrophy of the medial one, so that the morphological apex, and the appendix, lie close to the ileo-caecal junction. It is said to occur in 4 per cent. of adult subjects. In all cases the human caecum would appear to be less subdivided by indentations of its walls than we have shown above to occur in the Chimpanzee.

Representatives of all three primitive mesotyphla are normally recognizable in Man, but much confusion has arisen from the multiplicity of names that have been applied to them and to the fossae bounded by them. Some attempt was made by Berry (1897) to tabulate the synonymies, but unfortunately Berry himself adopted names that, however acceptable to anthropotomists, are not entirely suitable from the morphological aspect.

The intermediate mesotyphlon is macroscopically anangious and represented by the short, triangular or quadrilateral fold commonly known as the "bloodless fold of Treves". It is the ileo-caecal fold of Lockwood and Rolleston, a name also adopted by Berry. It is labelled ileo-appendicular in Gray's *Anatomy* (24th ed., 1930, p. 1236), a term derived from Jonnesco (1890), who, incidentally, did not regard it as free from vessels. Attached above to the antimesenteric wall of the ileum, it is connected distally to the left aspect of the caecum and inferiorly fades away on the anterior aspect of the meso-appendix. It therefore fails to gain the vermiform process. According to Berry it is absent in 10 per cent. of adults.

The sinistral fold is represented by the meso-appendix which is arranged exactly as described for the Pongidae. It carries, in its free margin, the appendical artery to the vermiform process, which vessel is quite independent from the caecal vessels. Between it and the "bloodless" fold is a peritoneal pouch that has received many names, the fashionable one being inferior ileo-caecal recess.

The dextral fold, usually named ileo-colic by human anatomists, is of more variable development. It was first noted by Luschka (1861), who observed its



association with a large branch of the ileo-colic artery. It presents a free border to the left, beneath which is a peritoneal recess of varying size, now termed superior ileo-caecal recess.

Beyond the fact that the caecum in Man is supplied by two branches from the ileo-colic artery, a smaller anterior and a larger posterior caecal branch, and that the appendix has its own vessel, text-books are extremely reticent on the question of the blood supply. It is difficult to gain information from the literature on the exact territories supplied by these various arteries. Treves informs us that the anterior vessel courses along the caecum in a curve, convex to the right, till it gains the anterior taenia, where it ends. He adds that many small branches come off its convex side, but none of any magnitude (often none at all) from its concave side. Treves evokes this arrangement as responsible for the asymmetrical growth of the caecum, probably with some justification. The same authority considered that the larger posterior artery was chiefly destined to supply the appendix. He avers that the appendicular vessel, coursing in or near the free edge of the meso-appendix, gives off, at regular intervals, a series of branches, only the first and largest of which is for the supply of the posterior wall of the caecum. Figures in English texts seem to be based on Jonnesco's diagrams published in Poirier and Charpy's *Anatomie humaine* (1895), wherein a more or less symmetrical distribution of anterior and posterior caecal vessels is shown. This arrangement does not logically follow on the comparative size of the two vessels and is not in agreement with what would be expected on the basis of the foregoing comparative studies, including that on the forms most nearly related to Man. On the other hand, Testut (8th ed., 1931) illustrates (figs. 436 and 437) the anterior vessel ramifying solely on the anterior caecal wall opposite the ileal attachment, and the posterior vessel supplying several large branches to the posterior wall. No indication is given of the source of blood supply to the more dependent parts of the anterior wall, but in a later figure (fig. 438), this is illustrated as coming from a much larger anterior caecal vessel, as in Jonnesco's figures. In the text the posterior artery is held responsible for the supply of a considerable proportion of the fundus of the caecum, sometimes even for the anterior surface thereof; it is also stated to anastomose with the anterior vessel. These statements are more in keeping with expectations from comparative anatomy, and no doubt are substantially correct as far as they go. In view of certain aberrations, it is interesting to note that the anterior vessel is stated on rare occasions to supply a branch which gains the root of the appendix (*vide infra*).

Rouvière (1924) figures a recurrent vessel from the appendicular artery proceeding into the "bloodless" fold. No doubt this variation is morphologically equivalent to the vessel responsible for the disposition of fat in the anterior tract on the appendix of the Pongidae, but which there fails to reach the bloodless fold. It is also comparable with the recurrent vessel observed in the intermediate meso-typhlon of *Colobus* and of some individuals of *Papio*, etc.

Clearly, some further investigation on the differential arterial supply of the human caecum is called for—more detailed than can be reported in a contribution of the scope of the present paper.

In two adult human caeca chosen at random, we find the anterior caecal artery following the course and distribution outlined by Treves. It gives, however, small

branches to the terminal ileum from its concave side. Its lateral branches disappear beneath the anterior taenia. It is not traceable inferiorly beyond a point just distal to the ileo-caecal entrance. The posterior caecal artery early breaks up into a leash of branches—eight or more in number, the uppermost to the colon, the lowermost to the dorsal aspect of the ileum and the intermediate ones to the dorsal surface of the caecum. The vessels tend to course in the sulci demarcating the haustra and are generally obscured by fat. They disappear beneath the posterior taenia—all except the lowest. This runs vertically downwards towards the root of the appendix; by-passing this by proceeding ventrally, it ends on the ventral aspect of the caecum, though not traceable very far on the surface, for it soon dives into the muscular wall of the gut. No doubt, therefore, as in lower Primates, the fundus of the caecum is supplied both dorsally and ventrally by vessels derived from the dorsal caecal system. No anastomosis has been noted between the dorsal and ventral systems. In both the specimens above referred to the “bloodless” fold was fatty and connected distally with the equally adipose meso-appendix—indicative of the presence of a recurrent blood-vessel derived from the appendicular artery. More detailed studies are in progress relative to the differential distribution of the caecal vessels in Man.

Before concluding this account of the human caecum and its adnexa, a note is required relative to two variations that we have met with that seem to have important morphological bearings. Both occurred in new-born infants.

The first, a male, possessed the usual symmetrical conical caecum tapering gradually to a long appendix like that retained in the adult *Hylobates*. The conical part of the caecum and the appendix, with its mesentery, were placed dorsal to the rest of the caecum and fixed in position by peritoneum forming around them a completely closed serous sac. This sac would, no doubt, have disappeared in the adult, to give the quite common retroperitoneal arrangement wherein all resemblance to typical Primate conditions is lost. The condition had clearly been brought about by fusion of the “bloodless” fold to the dorsal parietal peritoneum as part of the general meso-colic fusion. The appendicial mesentery with its contained vessels had been retained intact and unconnected with the walls of the sac. The usual fatty dextral fold was present.

The second specimen, from a female, was even more singular and necessitates a prior reference to a rare condition reported by Berry (1897), where, in a male aged two years, the “meso-appendix” was anterior in position and origin, arising from the anterior (*i.e.* dextral) layer of the enteric mesentery, passing inferiorly across the front of the ileum. Berry correctly surmises that this arrangement had been developed from an ileo-colic fold. In our example, which is of the same type (Pl. VI, fig. 27), the extensive dextral fold possesses a strong falciform free border directed to the left, and proceeding as far as the apex of the appendix. It carries the appendicial artery and, to the right of this, the anterior caecal artery, which is normally distributed. There is a large “bloodless” fold connected inferiorly with the dextral fold, the two folds forming the walls of a deep dextral peritoneal recess. Another shallower recess lies behind the “bloodless” fold, but the dorsal wall of this is formed of parietal peritoneum, for the sinistral fold is lacking, the posterior caecal vessels coursing entirely retroperitoneally. These supply the whole of the



dorsal aspect of the caecum, the lowest branch proceeding to the conical apex thereof, but not supplying the appendix. There has been substitution of dextral for sinistral vascular supply to the distal part of the caecum and the appendix, as normally happens in *Lagothrix* and some other Platyrrhine monkeys, and has been noted above to occur as an anomaly in the Orang.

It was not unexpectedly that we discovered in a specimen of complete visceral transposition (in the Anatomy Dept., Edinburgh) that the arrangements in the caecal region were the reverse of the normal, *i.e.* with a meso-appendix lying dorsally, a short "bloodless" fold (tending to split into laminae as observed in the Chimpanzee) and a short sinistral (*i.e.* ventral) fatty fold carrying "anterior" caecal vessels.

#### DISCUSSION.

##### 1. General: correlation with diet.

Many popular ideas on the anatomy of the caecal region are erroneous, yet die hard; for example, that the size and shape of the caecum depend largely on the diet of the animal, it being large in herbivores and small in carnivores.

The oft-quoted case of the rabbit, *Oryctolagus cuniculus*, is misleading, as its large caecum and "appendix" are highly specialized, not only in form but in function, being supposed to serve as a reservoir while digestion of cellulose takes place by the action of protozoa. The organ is quite different from that of other rodents, although the diet of many of these is similar. It is true that all the ungulates have large caeca and are all herbivorous, but this appears to us to be more characteristic of the morphological group than of the diet. Again, in the carnivorous Canidae, Felidae or Mustelidae the caecum is small or even absent, but in another group the diet may vary, yet the caecal form remains unchanged. Thus we have examined recently the Panda, *Ailurus fulgens*, and the Giant Panda, *Ailuropoda melanoleuca*, which are closely allied. The former, however, is almost omnivorous and will certainly take a largely carnivorous diet, while the latter is a truly vegetarian animal, which in nature probably exists entirely on bamboo shoots, and in captivity will tolerate very little else. Despite such differences in their diet, however, both animals have a very simple stomach and a coiled, small intestine leading straight into a short rectum without trace of a caecum. Raven (1936) also found no caecum in *Ailuropoda*.

These wider fields are mentioned merely to show the errors that may arise from the examination of a limited number of examples, even where differences of diet are more marked than among Primates. Other misconceptions will be mentioned in suitable connections later. It is hoped in further contributions to deal with caecal structure in other groups.

Among the Primates, however, marked differences of diet do occur between some closely-related groups. Attention has already been drawn to the speculations of Neuville regarding the diet of the Macaques (p. 223), but we find no difference between the caecum of *Macaca cyclopsis* living on hard, dry grass, etc., and such as *M. sinica* with a much more "juicy" diet. The omnivorous *Perodicticus* and *Nycticebus* have largely developed caeca, while the related *Arctocebus* with a short

caecum is carnivorous (Sanderson, 1940). The corollary is also true, for there is no relationship between the form of the caecum in species living on the same diet. Thus the Indriidae, *Alouatta* and the Colobidae are all leaf-eaters. Yet the Indriidae show very complex caeca; *Alouatta* has a short and simple one, while that of the Colobidae is intermediate in complexity and has its own specializations.

We find that among species with a similar diet, differences between the caeca are as great as between these and forms with a contrasted diet. Thus, the largely insectivorous *Tarsius*, *Loris* and *Perodicticus* show divergences greater than between *Perodicticus* and the vegetarian species of the Indriidae. Another example is the contrast between the short, almost rudimentary caecum of the bamboo-eating *Hapalemur* and the capacious organ of its two omnivorous relatives, *Lemur* and *Lepilemur*. In this—and we have chosen several of the same examples—we again differ from Neuville.

## 2. Correlated Specializations in the Gut.

Another possible clue to the wide range of variation in caecal form is its correlation with specialization and elaboration elsewhere in the gut. With regard to the stomach, this does not appear to hold, as instanced by the case of the Indriidae and Colobidae. The stomachs in Colobidae are the larger and more specialized, but their caeca are the more simple. This observation strikes at the root of a speculation by Barclay-Smith and Keith, based on small series of species, that the caecum acts as a "second stomach". Thus it should be large where the stomach is large, its function being presumed to be the temporary storage of gut contents which have passed rapidly through the small intestine preceding their delivery in quanta to the large intestine. This theory appeared to be confirmed by the discovery of a caecocolic sphincter or valve in certain forms (such as Man and *Callicebus*) and the demonstration by the early radiologists of peristaltic waves passing food from ileum to caecum, and others passing it from caecum to colon. Nevertheless, it must be again emphasized that no morphological evidence exists, in a comparative series of any size, for the general correctness of this theory, however true it may be in individual instances.

However, among the Primates, correlation of caecal form with colonic form can be demonstrated with ease, particularly caecal specialization with complexity of that part of the colon derived from the ansa. From the writings of others, an excellent example is found in the Indriidae as figured by Grandidier and Milne-Edwards. In all the genera of this family the ansa coli is greatly elongated, twisted spirally and further twisted forwards on itself and gains attachment to the oral and aboral segments of the colon by secondary peritoneal folds. The correlated elongation, twisting and elaboration of the caecum in these genera have been detailed above (p. 212).

Further, in the Galagos the colon is always rather complex and an interesting example of correlation with colonic complexity is shown in a group of closely-related species. In *Galago crassicaudatus* the ansa is long and bent on itself, in *G. senegalensis* var. this coiling is more marked, in *G. alleni* it is intermediate, but is most marked in *Euoticus*. The caeca of all these forms are large, but show an



increasing degree of complexity parallel with that of the colon, from the elongated tube with a twisted tip of *G. crassicaudatus* to the very long structure with spiral twists, sacculations, convolutions and a recurved tip with a special mesenteric attachment, found in *Euoticus*.

Another good example is from the Lorisidae. The ansa coli of *Nycticebus* is longer and more coiled than that of the *Loris*, while its caecum is not only longer but possesses a constricted, conical apex with thickened walls that has been compared with the human appendix (*vide supra*, p. 206).

The reverse of the above condition frequently holds good also, *i.e.* that a species with a very simple colon has a simple caecum. In our general introduction to the Cebidae, we noted that some had far simpler caeca than the Hapalidae. Thus, *Saimiri* has a very simple colon and caecum, the latter with a very primitive blood supply, the dextral vessel supplying only the terminal ileum and proximal colon, an arrangement which will be discussed in more detail below and shown to provide further evidence of the primitive nature of the caecum. In more advanced genera, such as *Pithecia*, the colon—and the caecum with it—are larger and more specialized than in the more primitive *Saimiri*, *Cebus* or *Aotes*. Even among these, the caecum of *Aotes* is the most specialized in correlation with its more complex colon. The presence of an "appendix" in *Aotes* serves only to emphasize this point. Moreover, in this genus the marked dilatation of the caecum goes with the large calibre of the colon.

The evidence is, therefore, complete, that as regards size and calibre the caecum bears no relation to the diet of the animal, but is part of the colon, subject to the same growth and metabolic gradients during ontogeny, gradients which often differ much from those affecting the mesogastric viscera.

From another aspect, this thesis is supported by the condition found in the Hominoidea. Here, especially in *Homo*, the colon has become much shorter than in lower forms, being fixed at the hepatic and splenic flexures, with no true ansa and even a progressive shortening of the ascending mesocolon to produce the fixed caecum characteristic of the Pongidae and Man. In all these, the true caecum is small, independent of the existence of the "appendix", and it would appear that its reduction must depend on the same factors as contribute to the secondary shortening of the colon. As regards such criteria as symmetry, blood supply, mesenteric arrangements and presence of an appendix, the caecum of the Hominoidea is far more specialized than that of *Saimiri*, though it is no larger proportionately.

### 3. *Specialization within the Caecum itself.*

Apart from size, the Primate caecum shows a wide range of specializations. One of the most obvious is its degree of asymmetry. Among the lowest forms, such specialization is obvious in the leftward convexity of that of *Loris* as opposed to the relatively symmetrical structure seen in *Tupaia*. However, in close allies of *Loris*, but with specializations developed better elsewhere in the colon, *e.g.* *Perodicticus*, the asymmetry is less marked, although in the varieties of *G. senegalensis* this reappears. In the Hapalidae also, asymmetry occurs in some, but appears to be distributed capriciously with regard to other features. Thus, in *Mytax* and

*Leontocēbus* the organ is straighter than in *Hapale*. It varies greatly in the Catarrhines. Thus the caecum of *Macaca* and *Cercocebus* is definitely asymmetrical, being curved to the left; *Papio*, *Mandrillus* and *Cercopithecus* show less curvature, while *Erythrocebus* shows hardly any.

Asymmetry is, of course, due to a progressive growth in length of the wall forming the convexity. It is the morphological cranial wall which elongates, as is well demonstrated in the series of Hominoidea. Thus the Hylobatidae have a more symmetrical caecum than the Pongidae and their appendix arises from the most dependent part. In *Pongo* and *Anthropopithecus* the asymmetry is more marked, reaching its limit in the normal adult type of *Gorilla* and *Homo*. Even here much of the asymmetry develops after birth, for many human adults possess the infantile, more symmetrical type of caecum (Type Two of Treves).

#### 4. Proximo-distal Specialization of the Caecum.

Another type of specialization which appears to us independent of asymmetry, at least in part, is proximo-distal differentiation resulting in an obvious difference in calibre between the two ends. Usually they differ in structure as well. The criteria by which an "appendix" can be differentiated have been set out above in the Introduction (p. 200) and need not be repeated. All the "appendices" described here appear to represent the morphological distal moiety of the whole caecum—however much they may be bent or twisted. In *Nycticebus* a simple narrowing of the terminal portion of a straight and symmetrical viscus has been recorded. An even less-marked but distinct narrowing is seen in *Galago crassicaudatus*, but in the last-mentioned this terminal portion is bent on itself. In *Euoticus* the narrowing is not abrupt, but the narrow portion is sharply curved and held in place by a special fold of peritoneum. *Daubentonia* is another example. In all of the above, no difference in the longitudinal muscle coats of the two parts of the caecum is found (except sometimes in *Nycticebus*).

In the Hapalidae the caecum is hook-shaped, but the apex is blunt. Here, however, the specialization noted by Berry occurs, namely a concentration of lymphoid tissue at the apex, e.g. in *Mystax*. This modification seems to be a side branch among the Platyrrhines, whose specializations deserve further discussion later. It recurs, however, in the Baboons, where a definite terminal "bosselure" (Broca) is common. This type of caecum is more symmetrical at birth than in adult life, and its terminal part is covered with a complete coat of longitudinal muscle, the taeniae converging to form this. In many of the lower Primates, of course, the whole caecum possesses a complete coat of longitudinal muscle. The increasing specialization of the terminal part is well seen in the Colobidae, especially in *Semnopithecus*, where it is found even in the embryo, although at this stage the caecum is less asymmetrical than in the adult. The level of the division is, in this family, so far proximal that the distal portion is by far the larger. In this respect they are unique. In *Kasi* the taeniae have met about half-way down the caecum, but proximal even to this in *Colobus*.

Below the Hominoidea, extreme narrowing of the caecal apex is seen best among certain Cebidae. The best example is *Aotes*, while in *Callicebus* the narrow portion may or may not be sharply constricted off from the rest, according to the state of muscular contraction.



The most advanced instances of this specialization admittedly occur in the Hominoidea. Thus the Hylobatidae all show both the narrowing and the convergence of the taeniae, but the narrowing is not as abrupt as in *Pongo*, where the super-added asymmetry of the viscus accentuates the marked difference between what are really two parts of the same organ, i.e. the "caecum" proper and the "vermiform appendix". Further proximo-distal differentiation by the concentration of all lymphoid tissue in the appendix of *Homo* is well known, but we have found some such tissue retained by a human caecum. As noted above, this concentration occurs to some extent in Hapalidae and Baboons. Much of our material may not have been well enough preserved to show this in other instances.

From these findings the vermiform termination of the caecum of the Hominoidea is indubitably merely a more advanced degree of the modification of the caecal apex seen in many lower Primates, especially the terminal "bosselure" of the Baboons, the upturned termination found in many of the Lorisoidea, Hapalidae and *Lagothrix*, and of the distinct structure found in *Aotes*. That this terminal portion is more distinct in the Hominoidea is merely an indication of the increased specialization and is definitely no evidence of a degenerative nature.

Obviously we must not be committed to a structure of vermiform appearance before it can be labelled an appendix. The shape matters little, so long as morphological criteria are satisfied. In these circumstances we submit that the term "appendix vermiformis" should be dropped, at least in comparative anatomy. The correct term for this structure is "appendix caecalis".

Further evidence that the human appendix is not undergoing phylogenetic degeneration is that in the embryo it grows steadily and continuously with no regression at any stage (Gluckman, 1946 b).

### 5. *The Mesotyphlon.*

Throughout the descriptive part of this paper it has been shown how the mesotyphla of all the examples quoted can be fitted into the primitive scheme outlined in the Introduction. It will be obvious how their arrangement is modified by such purely "mechanical" factors as the angle between the caecum and ileum and their relative sizes. We regard the arrangement in such otherwise primitive genera as *Tupaia*, *Tarsius* and *Microcebus* as specialized, although only two folds are present, the sinistral vessels running in a median fold. We do this because the triple arrangement persists throughout all the other members of the Order, even where very specialized as in the Pongidae, in which the sinistral and intermediate folds persist, although modified in varying degrees—even between individuals of the same species—by the shortening of the mesocolon and the fixation of the caecum to the posterior abdominal wall. It may well be that the formation of a sinistral fold is a specialization, on evidence gathered from the Primates. The sinistral vessels are almost invariably the larger, but there seems no reason apart from this why this fold should persist in such unusual circumstances.

Among genera with triple folds the most primitive would appear to be *Saimiri* with its symmetrical arrangement of small plicae. *Nycticebus* is simple also, in contrast to the closely-related *Loris*—a point of interest in view of the fact that its colon is the more specialized. In *Ateles* alone both the folds and the vessels are,

according to Treves and Huntington, of the same size. In *Lagothrix* always, and sometimes also in *Aotes*, *Pongo* and *Homo*, the dextral vessel and fold are the larger. It would appear that the correlation of size of vessel and fold is not always complete, the left fold being more persistent than the right, even when the need for it is reduced, e.g. in Hominoidea.

It will be recalled that *Macroscelides* is unique in having no dextral or sinistral fold which may indicate that the double fold in *Tupaia* is primitive after all.

As regards the relationship of the folds to the appendix caecalis, in the primitive condition this is connected to the median anangious fold. However, most primitive appendices arise distal to any attachment of the membrane, e.g. *Galago crassicaudatus*, *Hapale santaremensis* and *Aotes*. In *Pongo*, *Anthropopithecus* and *Gorilla* a remnant of the median attachment seems to persist, detached from the meso-appendix, which might lead to the conclusion that, in these animals, this viscus represents a relatively large proportion of the original caecum.

The mesenteries of the most specialized appendices caecales are all derived from the fold carrying the main blood vessel to the viscus. Even in the great apes mentioned in the last paragraph, this meso-appendix is found in addition to the median fold. Since the main vessel of supply to the caecum is typically the sinistral one, it is the sinistral fold which runs to the appendix when this is not attached solely to the median. In one of our examples of *Aotes*, one Orang-utan and several humans, the dextral vessel was the main one and the appendix consequently slung from the dextral fold.

The median fold and that carrying the main vessel can readily fuse. Thus, in *Loris*, the main sinistral artery runs into the median fold without raising a ridge of its own. As mentioned above, this cannot be explained on "mechanical" grounds, since there is nothing peculiar in the form of the caecum as compared with that of allied forms with a definite dextral fold. The case of *Lemur* and *Lepilemur* is even more interesting, since not only is the dextral fold small, but so is the median one, and this soon fuses with the large sinistral fold, much in the same way as happens in some human individuals when the ileo-caecal recess is found to be obliterated. In *Lemur*, therefore, the main mesotylphlon is the sinistral fold and it is easy to see from this how, when the terminal part of the caecum forms an appendix, the latter is associated with the fold carrying the largest vessel.

In *Pithecia* and also one of our examples of *Papio*, sinistral vessels enter the primarily anangious median fold, while in the former, the sinistral fold is poorly developed. The same condition is found in *Galago crassicaudatus* and *G. demidovii*. In Man a small branch from the appendicular artery often enters the intermediate fold, which is, therefore, not bloodless "except in the sense that its origin (is) not determined by blood-vessels" (Kelly and Hurdon).

#### 6. Arteries.

Distribution of the caecal arteries has received little attention hitherto, and is not adequately known even for *Homo*. *Ateles* is the only Primate for which a symmetrical distribution of the sinistral and dextral vessels has been claimed (Treves, Huntington). In its nearest ally, *Lagothrix*, we find the dextral vessel to be the principal vascular channel to the caecum and to be responsible for the entire supply



of its distal moiety. In this respect the genus is unique, except for certain examples of *Aotes* and, as an aberration, in *Pongo* and *Homo*. These instances apart, the vascular supply of the caecal region may categorically be stated to show a remarkable degree of asymmetry, the sinistral vessel being far larger than the dextral, supplying the major part of the blind gut; and this arrangement prevails from *Tupaia* upwards to *Homo*. In some forms (e.g. *Saimiri*, *Daubentonia*) the dextral artery is so reduced that it can scarcely be said to enter the territory of the caecum, being confined to the area opposite the ileo-colic junction and the neighbouring part of the colon. More usually, it gives a recurrent branch to the terminal ileum and a variable contribution to the proximal part only of the ventral (dextral) wall of the caecum. The caecal contribution may or may not enter into anastomosis with the system derived from sinistral vascular channels. In *Pithecia*, for example, the two systems are very distinct and clearly separated (Pl. V, fig. 19), and the same applies in some measure to *Nycticebus* and *Microcebus*. In some Galagidae, however, and in *Colobus*, an anastomotic channel is developed connecting the two systems. Elsewhere, anastomoses if present, are not visible to the unaided eye.

It follows that the territory of the sinistral caecal artery typically includes the whole of the sinistral (dorsal) wall of the caecum from base to apex, and in addition, such parts of the ventral (dextral) wall as are not vascularized by the dextral artery. This territory, therefore, includes the whole of the apical region and generally involves more of the blind gut than is taken up in the formation of an appendix caecalis, whether this be macroscopically manifest or not. This inference is borne out by the detailed distribution of the caecal arteries of the Hominoidea, in which the vermiform appendix is provided with its own artery derived directly from the ileo-colic prior to the emergence of the posterior caecal. Nevertheless the last mentioned contributes a ventral branch in *Pongo*, *Anthropopithecus* and *Homo*. In *Homo* this branch crosses the morphological median line of the lesser curvature of the caecum just proximal to the appendical root, supplying, thereafter, a variable amount of the ventral aspect and fundus of the right (lateral) sacculum of the caecum proper. We find that this branch, which would appear to correspond to that termed caeco-appendicular by Kelly and Hurdon, also contributes a twig to the basal half inch of the appendix. The vessel of the junctional region is therefore, in our experience, a derivative of the posterior caecal and not, as Kelly and Hurdon maintain, of the appendical, though no doubt individual variants are frequent, provided a sufficiently large number are examined. The recurrent artery sometimes found in the free edge of the "bloodless fold" of Treves is a derivative, in the Hominoidea, of this caeco-appendicular vessel, and is so figured by Kelly and Hurdon.

A consideration of the arterial supply of the caecal area of the Hominoidea leads to the inference that the appendix is nothing but a modified part of the caecum and represents, indeed, probably the major part of the length of the large caecum of the Strepsirhini, the Hapalidae and some Cebidae. It follows then that the caecum proper of the Hominoidea is, for all practical purposes, nothing more or less than that part of the total caecum of the lower forms, whereof the dextral wall is vascularized by the homolateral caecal artery and which has undergone a peculiar growth pattern, increasing in calibre and enlarging asymmetrically at the expense of that

part of the viscus whose ventral wall is nourished by the hetero-lateral vessel. In the special case of *Saimiri* and a few others it would appear that this part of the organ, so well developed in Man, is reduced almost to disappearance, and their total caecum corresponds morphologically only with the appendix caecalis of higher forms.

It is curious that a parallel may be drawn between the human caecum and that of *Lemur*, where the median mesotyphlon runs into the sinistral fold which carries the main blood supply. In such a form as this, the identity of the human appendix with the whole of the caecum of the lower form becomes more obvious.

#### SUMMARY AND CONCLUSIONS.

The caecal region of almost all genera and most species of the Primates has been examined. The gross external anatomy is described with particular reference to mesenteries and blood supply, as well as to the form of the organ and its muscular coats. Very great differences of form were found.

Almost all have three mesenteries, viz. :—a median fold, primarily anangious, and others on the morphologically sinistral and dextral sides bearing arteries. The artery in the sinistral fold is usually the larger. This arrangement persists even in the most specialized and modified cases.

Complexity of the caecum is not related to diet, but to complexity of the colon ; where the colon is secondarily simplified, the caecum is reduced in size and complexity, although more specialized in other respects.

Asymmetry of the caecum is not related to other specializations.

At all levels within the Order, specialization of the distal part of the viscus may occur with the formation of an appendix caecalis. The "vermiform appendix" of the Hominoidea is the most specialized of these and its homology with similar structures in lower forms is confirmed by the arrangement of its mesenteries and arteries. It is certainly not a degenerate structure.

#### ACKNOWLEDGMENTS.

We have to thank the Zoological Society of London for access to a number of the specimens described, and Prof. A. J. E. Cave, Prof. F. Wood-Jones and Mr. T. C. S. Morrison-Scott for others. Many specimens were preserved and injected by Mr. W. E. Lawrence of the Zoological Society's Prosectorium. The illustrations were drawn with meticulous accuracy and unremitting care by Mrs. W. C. Osman Hill.

We should particularly like to express our indebtedness to the Royal Society and the Carnegie Trust for the Universities of Scotland for grants towards the cost of the plates.

#### ADDENDUM ON *ARCTOCEBUS CALABARENSIS*.

(*Vide supra*, p. 205.)

Since the foregoing was written it has been our good fortune, through the kindness of Dr. E. Hindle, Dr. G. M. Ververs and Mr. T. C. S. Morrison-Scott, to receive a spirit specimen of the trunk, with well preserved viscera, of a female *Arctocebus calabarensis* collected by Mr. Durrell in the Cameroons.



Examination shows our surmise to be correct in reference to the simple nature of the ansa coli, which closely resembles that of *Loris*, but which is rather longer. The colon is unsacculated. Huxley's description of the caecum, however, is quite inadequate. In our specimen this is very capacious and much longer than depicted in Huxley's figure. It is, indeed, longer than the "ascending colon" and equal to or exceeding it in calibre, except at its apex, which forms a blunt, rounded cone. The junction of the caecum with the colon is constricted, but behind this it balloons out into a succession of sacculations, separated from each other by annular sulci completely encircling the gut, for there is no concentration of the longitudinal muscular fibres to form taeniae. The terminal segment of the ileum is dilated and enters the colon at an obtuse angle; it likewise is constricted at its union with the colon.

An extensive triangular intermediate mesotyphlon is present, connecting the antimesenteric border of the ileum with the left wall of the caecum, extending along the latter for about half its total length. The fold is not completely anangious, for it contains a few veins, but no recurrent artery could be detected. The principal vessel supplying the caecum is a large sinistral artery descending in a peritoneal plica across the dorsal aspect of the ileo-caecal junction. It proceeds across the dorsal surface of the mesotyphlon, near the caecal border of the latter, and proceeds within a raised peritoneal fold running parallel with but separate from the caecal border of the mesotyphlon. It courses subserously to the apex caeci and supplies branches to dextral and sinistral walls of the viscus. A small dextral artery arising from the anterior mesenteric crosses the ileo-caecal junction subserously and supplies the dextral wall of the basal sacculaton only of the caecum, without obvious anastomosis with the branches of the sinistral artery.

#### REFERENCES TO LITERATURE.

- BARCLAY-SMITH, E. (1902). A Case of Extreme Visceral Dislocation; with remarks on the Functional Interpretation of the Agminated Glands of the Intestine. *Proc. Camb. phil. Soc.* **12**, 18-26.
- BEATTIE, J. (1927). The Anatomy of the Common Marmoset (*Hapale jacchus*, Kuhl). *Proc. zool. Soc. Lond.* **1927**, 593-718.
- BEDDARD, F. E. (1884). On some points in the structure of *Hapalemur griseus*. *Proc. zool. Soc. Lond.* **1884**, 391-399.
- BEDDARD, F. E. (1891). Additional notes upon *Hapalemur griseus*. *Proc. zool. Soc. Lond.* **1891**, 449-461.
- BEDDARD, F. E. (1901). Notes on the Broad-nosed Lemur, *Hapalemur simus*. *Proc. zool. Soc. Lond.* **1901** (1), 121-129.
- BEDDARD, F. E. (1908 a). On the Anatomy of *Antechinomys*, etc. *Proc. zool. Soc. Lond.* **1908**, 561-605.
- BEDDARD, F. E. (1908 b). Some notes upon the Anatomy of *Chiromys madagascariensis*, with reference to other Lemurs. *Proc. zool. Soc. Lond.* **1908**, 694-702.
- BEDDARD, F. E. (1909 a). *Mammalia in Cambridge Natural History*.
- BEDDARD, F. E. (1909 b). Notes upon the Anatomy of Monkeys of the Genus *Pithecia*. *Proc. zool. Soc. Lond.* **1909**, 928-943.
- BERRY, R. J. A. (1897). *The Caecal Folds and Fossae*. Edinburgh.
- BERRY, R. J. A. (1901). The True Caecal Apex or Vermiform Appendix: its Minute and Comparative Anatomy. *J. Anat. Lond.* **35**, 83-100.
- BRADLEY, O. C. (1903). On the Abdominal Viscera of *Cercocebus fuliginosus* and *Lagothrix humboldti*. *Proc. roy. Soc. Edinb.* **24**, 505-543.
- BROCA, P. (1869). L'Ordre des Primates. *Bull. Soc. Anthropol. Paris* (2) **4**, 228-401.

- CHAPMAN, H. C. (1880). On the Structure of the Orang-outang. *Proc. Acad. nat. Sci. Philad.* **1880**, 160-175.
- CHAPMAN, H. C. (1900). Observations upon the Anatomy of *Hylobates leuciscus* and *Chiromys madagascariensis*. *Proc. Acad. nat. Sci. Philad.* **1900**, 414-423.
- CLARK, W. E. LE GROS (1926). On the Anatomy of the Pen-tailed Tree-shrew (*Ptilocercus lowii*). *Proc. zool. Soc. Lond.* **1926**, 1179-1309.
- CLARK, W. E. LE GROS (1934). *Early Forerunners of Man*. London.
- DENIKER, J. (1884). Sur un Foetus de Gorille. *C.R. Acad. Sci. Paris*, **108**, 753-756.
- DUCKWORTH, W. L. H. (1904). *Morphology and Anthropology*. 1st ed., Cambridge.
- DUCKWORTH, W. L. H., & ELLIOT, T. R. (1904). Notes on the Pelvic and Abdominal Organs and Anatomy of *Galago garnetti*. *Stud. anthrop. Lab. Anat. Sch. Cambridge*, 54-60.
- EGGELING, H. VON (1920). In wie weit ist der Wurmfortsatz am menschlichen Blinddarm ein rudimentäres Gebilde? *Anat. Anz.* **53**, 401-428.
- FORBES, W. A. (1880). On the External Characters and Anatomy of the Red Ouakari Monkey (*Brachyurus rubicundus*); with remarks on the other species of that genus. *Proc. zool. Soc. Lond.* **1880**, 627-647.
- FLOWER, W. H. (1872). Lectures on the Comparative Anatomy of the organs of digestion of the Mammalia. *Med. Times Lond.* (1), 215-219.
- GARROD, A. H. (1879). Notes on the Anatomy of *Gelada ruepelli*. *Proc. zool. Soc. Lond.* **1879**, 451-457.
- GLUCKMANN, F. (1946 a). Les Formations nerveuses géantes de l'Appendice du Chimpanzé, *Troglodytes niger*. *C.R. Acad. Sci. Paris*, **223**, 555-557.
- GLUCKMANN, F. (1946 b). Evolution de l'Appendice Embryonnaire. L'Appendice Primordiale Caduc. *C.R. Acad. Sci. Paris*, **223**, 594-596.
- GRATIOLET, L. P., & ALIX, P. H. E. (1866). Recherches sur l'Anatomie du *Troglodytes aubryi*, Chimpanzé d'une espèce nouvelle. *Nouv. Arch. Mus. Hist. nat. Paris*, **2**, 1-264.
- HARROWER, G. (1933). *Nycticebus malaianus* Anderson. A dissection of the Abdomino-pelvic Viscera. *Ceylon J. Sci. (B)*, **18**, 73-87.
- HERVÉ, C. (1882). De l'Existence d'un Appendice Caecal Rudimentaire chez quelques Pitheciens. *Bull. Soc. Anthropol. Paris*, **5**, 792-794.
- HILL, W. C. OSMAN (1936). The Affinities of the Lorisoidea. *Ceyl. J. Sci.* **19 B**, 287-314.
- HUNTER, R. H. (1936). The Ganglionic Tissue of the Ileo-caecal Junction. *Ulster med. J.* **5**, 54-57.
- HUNTINGTON, G. S. (1903). *The Anatomy of the Human Peritoneum and Abdominal Cavity*. Philadelphia and New York.
- HUXLEY, T. H. (1864). On the Angwantibo (*Arctocebus calabarensis* Gray) of Old Calabar. *Proc. zool. Soc. Lond.* **1864**, 314-335.
- JACOBSSHAGEN, E. (1923). Zur Morphologie des menschlichen Blinddarms. *Anat. Anz.* **56**, 97-133.
- JACOBSSHAGEN, E. (1930). Das Schleimhautrelief des Prosimier-Rumpfdarms mit Beiträgen zur Kenntnis der Kerkringschen Faltensysteme der Anthropoiden und des Menschen. *Jena. Z. Naturw.* **64**, 1-90.
- JOHNSTON, T. B. (1920). The Ileo-caecal region of *Callicebus personatus*. *J. Anat. Lond.* **54**, 66-78.
- JOHNSTON, T. B. (1930). *Gray's Anatomy, descriptive and applied*. 24th ed., London.
- JONNESCO, T. (1890). *Hernies Internes Rétro-péritoneales*. Paris.
- JONNESCO, T. (1895). In Poirier and Charpy, *q.v.*
- KEITH, A. (1891). Anatomical notes on Malay Apes. *J. Straits Br. Asiat. Soc.* **1891**, 77-89.
- KEITH, A. (1904). Anatomical evidence as to the nature of the Caecum and Appendix. *Proc. Anat. Soc. Lond.* **1903**, vii-xx.
- KEITH, A. (1912). Functional nature of the Caecum and Appendix. *Brit. med. J.* **2**, 1599-1602.
- KEITH, A. (1915). An account of six specimens of the Great Bowel removed at operation: with some observations on the motor mechanism of the Colon. *Brit. J. Surg.* **2**, 576-599.
- KELLY, H. A., & HURDON, A. (1905). *The Vermiform Appendix and its diseases*. Philadelphia and London.
- KLAATSCH, H. (1892). Zur Morphologie der Mesenterialbildungen und des Darmkanals. *Morph. Jb.* **18**, 665-716.
- KOHLBRUGGE, J. H. F. (1891). Versuch einer Anatomie des Genus *Hylobates*. *Weber's Zool. Ergebn. Reise Niederländ. Ost-Ind.* **1**, 211-354.



- LOCKWOOD, C. B., & ROLLESTON, H. D. (1891). The Fossae round the Caecum and the position of the Vermiform Appendix, with special reference to Retro-peritoneal Hernia. *J. Anat. Lond.* **26**, 130-148.
- LOGHEM, J. J. VAN (1903). Das Colon und Mesocolon der Primaten. *Ned. Bijd. Anat.* **2**, 350-437.
- LOVE, R. J. MCN. (1947). *The Appendix*. London.
- LUSCHKA, H. VON (1861). Ueber die Peritoneal Umhüllung des Blinddarmes und ueber die Fossa Ileo Caecalis. *Virchow's Archiv.* **21**, 285-288.
- MARTIN, W. (1833 a). Note of the dissection of a Slender Loris (*Loris gracilis* Geoffr.). *Proc. zool. Soc. Lond.* **1833**, 22-24.
- MARTIN, W. (1833 b). Notes on the dissection of a Squirrel Monkey (*Callithrix sciureus* Geoffr.). *Proc. zool. Soc. Lond.* **1833**, 88-90.
- MARTIN, W. (1835). Notes on the dissection of a small Nocturnal Lemur (*Microcebus murinus* Geoffr.). *Proc. zool. Soc. Lond.* **1835**, 125-127.
- MILNE-EDWARDS, A., & GRANDIDIER, A. (1876, 1890). *Histoire Physique, Naturelle et Politique de Madagascar. Histoire Naturelle des Mammifères*, **6** (text), **9** (atlas).
- MITCHELL, P. C. (1905). On the Intestinal Tract of Mammals. *Trans. zool. Soc. Lond.* **17**, 437-536.
- MITCHELL, P. C. (1916). Further observations on the Intestinal Tract of Mammals. *Proc. zool. Soc. Lond.* **1916**, 183-250.
- NEUVILLE, H. (1922). Signification de l'Appendice Vermiculaire des Primates. *Anthrop. Paris*, **32**, 409-451.
- OPPEL, A. (1897). *Mikroskopische Anatomie*. **2**, Jena.
- OWEN, R. (1863). On the Aye-aye (*Chiromys* Cuvier). *Trans. zool. Soc. Lond.* **5**, 33-101.
- OWEN, R. (1868). *Comparative Anatomy and Physiology of Vertebrates*. **3**, London.
- PETERS, W. C. H. (1865). Ueber die Säugethiergattung *Chiromys* (Aye-aye). *Abh. preuss. Akad. Wiss. (Physik. Abt.)*, **1865**, 79-100.
- POIRIER, P., & CHARPY, A. (1895). *Traité d'Anatomie Humaine*. Paris, **4**, fasc. i, 320.
- RAVEN, H. C. (1936). Notes on the anatomy of the viscera of the giant panda (*Ailuropoda melanoleuca*). *Amer. Mus. Nov.* **177**, 1-23.
- REIDER, N. (1936). The Primate Colon. *Proc. zool. Soc. Lond.* **1936**, 433-453.
- ROUVIÈRE, H. (1924). *Anatomie Humaine*. Paris, **1**, 780.
- SANDERSON, I. T. (1940). The Mammals of the North Cameroons Forest area. *Trans. zool. Soc. Lond.* **24**, 623-725.
- SCHWARZ, E. (1931). Revision of the Genera and Species of Madagascar Lemuridae. *Proc. zool. Soc. Lond.* **1931**, 399-428.
- SMITH, A. (1849). *Illustrations of the Zoology of South Africa. Mammalia*. London.
- SONNTAG, C. F. (1924). *Morphology and Evolution of the Apes and Man*. London.
- STRAUS, W. L. (1936). Thoracic and Abdominal Viscera of Primates, with special reference to the Orang-utan. *Proc. Amer. phil. Soc.* **76**, 1-85.
- TESTUT, L. (1931). *Traité d'Anatomie Humaine*. Paris, 8 ed. (revised by A. Latarjet), **4**, 397-433.
- TREVES, F. (1885). The Anatomy of the Intestinal Canal and Peritoneum. *Brit. med. J.* **1**, 415-419, 470-474, 527-530, 580-583.
- WEINBERG, M. (1906). De l'Existence de l'Appendice chez les Singes Inférieurs. *C.R. Soc. Biol. Paris*, **60**, 844-845.
- WELDON, W. F. R. (1884). Notes on *Callithrix gigot*. *Proc. zool. Soc. Lond.* **1884**, 6-9.
- WOOD-JONES, F. (1929). *Man's place among the Mammals*. London.

PLATE I.



## PLATE I.

- Fig. 1. *Tupaia (Anathana) ellioti*, male. Ileo-caecal region and large intestine from the ventral aspect, with related peritoneal membranes and associated vessels. 1, Intermediate mesotyphlon; 2, sinistral mesotyphlon; *Du*, cut end of duodenum; *D*, dextral caecal artery; *S*, sinistral caecal artery.
- Fig. 2. *Tarsius borneanus*, male. Ileo-caecal region and large intestine from the ventral aspect. References as in Fig. 1.
- Fig. 3. *Microcebus murinus murinus*, female. Ileo-caecal region and large intestine from the ventral aspect. 3, dextral mesotyphlon. Other references as in preceding figs.
- Fig. 4. *Loris tardigradus tardigradus*. Ileo-caecal region and large intestine from the ventral aspect. *A*, ansa coli; *AL*, anso colic ligament. Other references as in preceding figs.
- Fig. 5. *Nycticebus coucang coucang*. Ileo-caecal region and large intestine from the ventral aspect. The ansa coli has been displaced to the right to expose the ileo-caecal area. The sinistral vessel *S* is seen through the transparent, anangious median mesotyphlon. References as in preceding figs.
- Fig. 6. *Perodicticus potto*, male. Ileo-caecal region and large intestine from the ventral aspect. A large part of the ansa colic membrane has been removed to expose the ileo-caecal area. Its line of attachment to the proximal colon and caecum is marked at *X*. References as in preceding figs.





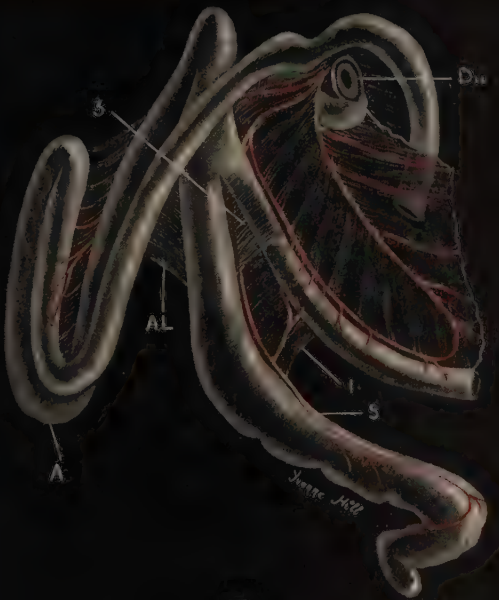


PLATE II.



## PLATE II.

- Fig. 7. *Galago crassicaudatus argentatus*, male. Ileo-caecal region and large intestine from the ventral aspect. The ansa coli has been displaced to the right to expose the ileo-caecal area. References as in preceding figs.
- Fig. 8. *Galago senegalensis braccatus*, female. Ileo-caecal region from the ventral aspect. References as in preceding figs.
- Fig. 8 a. *Euoticus elegantulus pallidus*, male. Ileo-caecal region and large intestine from the ventral aspect. References as in preceding figs.
- Fig. 9. *Lemur fulvus*, female. Ileo-caecal region and large intestine. Note the fatty nature of the dextral mesotyphlon. References as in preceding figs.



7



8



8A



9





PLATE III.



## PLATE III.

- Fig. 10. *Lepilemur mustelinus*. Ileo-caecal region and proximal part of large intestine from the ventral aspect. The ansa coli has been displaced to the right to expose the ileo-caecal area. Modified from Milne-Edwards and Grandidier. References as in preceding figs.
- Fig. 11. *Daubentonia madagascariensis*, female. Ileo-caecal region and large intestine from the ventral aspect. From a specimen in the Royal College of Surgeons of England. References as in preceding figs.
- Fig. 12. *Propithecus diadema*, male foetus. Ileo-caecal region and large intestine from the ventral aspect. Part of the colic labyrinth has been displaced to the right. References as in preceding figs.
- Fig. 13. *Mystax midas*, male. Ileo-caecal region and large intestine from the ventral aspect. The mesentery and the two lateral mesotyphla were fatty in this specimen; but note transparent nature of intermediate mesotyphlon. References as in preceding figs.
- Fig. 14. *Hapale jacchus*, male. Ileo-caecal region and large intestine from the ventral aspect. *AC*, appendix caecalis. The inset figure shows the ileo-caecal junction of another specimen (female) from the medial aspect indicating the delamination of the intermediate mesotyphlon into three separate membranes, flanked by fatty dextral and sinistral mesotyphla. Other references as in preceding figs.

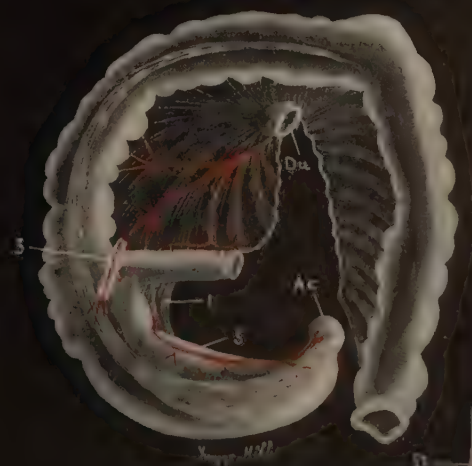
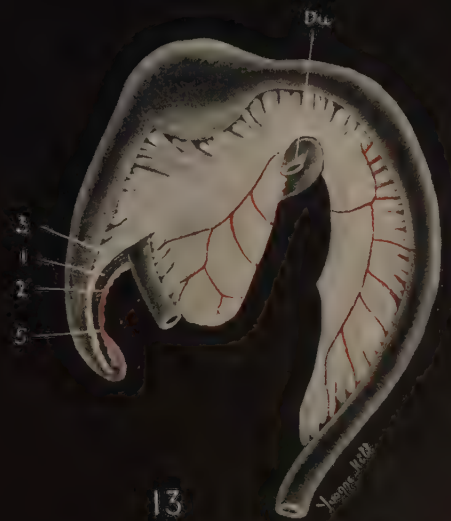
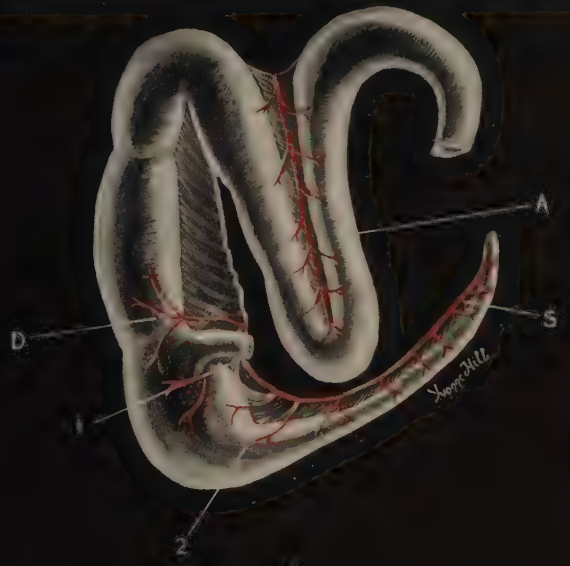






PLATE IV.



## PLATE IV.

- Fig. 15. *Hapale santaremensis*, male. Ileo-caecal region and large intestine from the ventral aspect. References as in preceding figs.
- Fig. 15 a. *Oedipomidas geoffroyi*, male. Ileo-caecal region and large intestine from the ventral aspect. References as in preceding figs.
- Fig. 16. *Saimiri sciurea*, male. Ileo-caecal region and large intestine from the ventral aspect. The inset shows the dorsal aspect of the ileo-caecal junction after displacement of the caecum caudally and to the left. *lg*, lymph glands. Other references as in preceding figs.
- Fig. 17. *Cebus xanthosternos*, male. Duodenum, ileo-caecal region and large intestine from the ventral aspect. References as in preceding figs.
- Fig. 18. *Aotes zonalis*, male. Ileo-caecal region and large intestine from the ventral aspect. Note the substitution of the dextral for the sinistral as the principal artery of supply of the caecum. References as in preceding figs.
- Fig. 18 a. Caecum, etc., in ventral view, of : *A*, *Callicebus gigot* ; *B*, *C. moloch* and *C*, *C. personatus*. (*A* and *B* adapted from Weldon, *C* adapted from Johnston.)

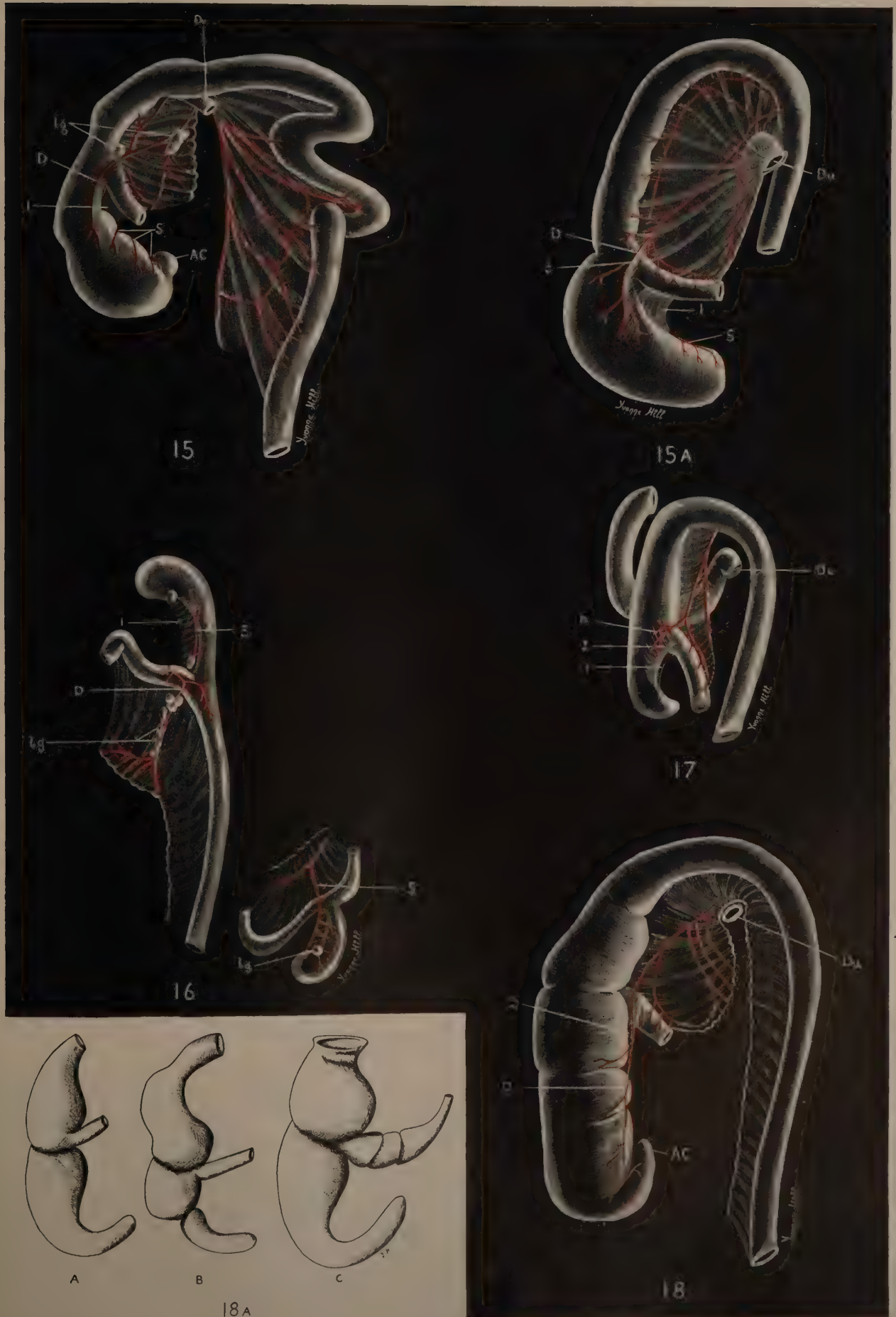




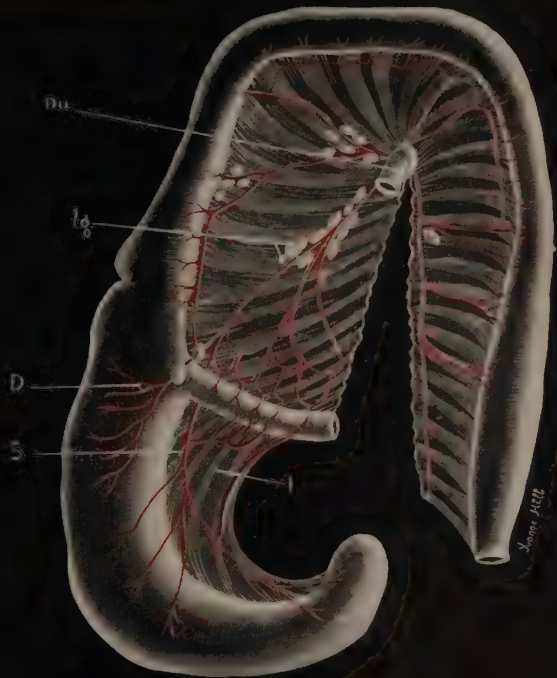


PLATE V.



## PLATE V.

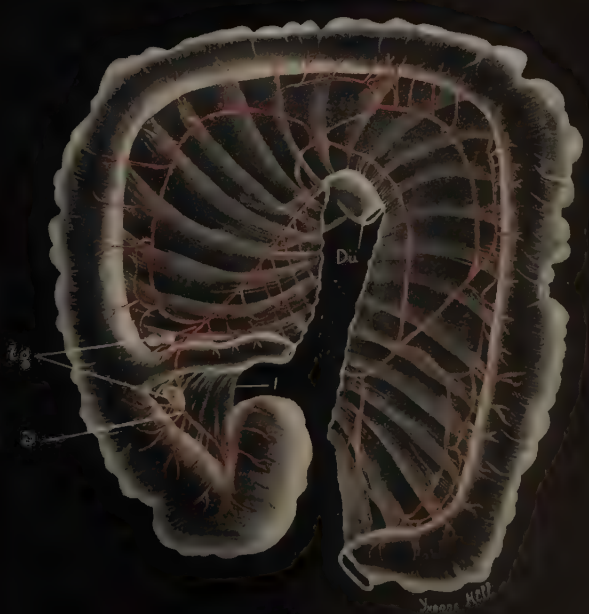
- Fig. 19. *Pithecia monachus*, female. Ileo-caecal region and large intestine from the ventral aspect. References as preceding figs.
- Fig. 20. *Alouatta seniculus*, male. Ileo-caecal region and large intestine from the ventral aspect. References as in preceding figs.
- Fig. 21. *Lagothrix humboldti*, male. Ileo-caecal region and large intestine from the ventral aspect. References as in preceding figs.
- Fig. 22. *Papio papio*, female. Ileo-caecal region from the ventral aspect. *AC*, rudimentary appendix caecalis. Other references as in preceding figs.



19



20



21



22



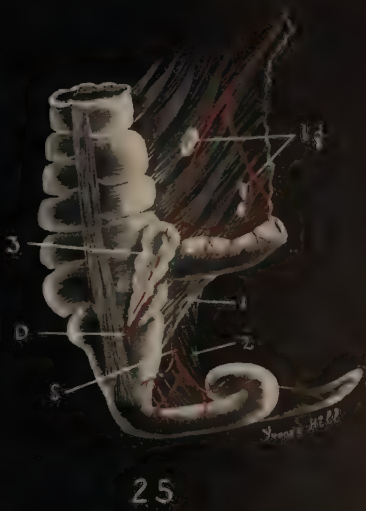
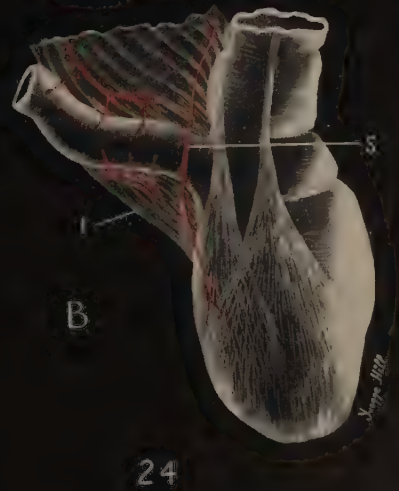


PLATE VI.



## PLATE VI.

- Fig. 23. *Kasi senex nestor*. Ileo-caecal region and large intestine from the ventral aspect. References as in preceding figs.
- Fig. 24. *Colobus abyssinicus matschiei*, male. Ileo-caecal region from *A*, ventral, and *B*, dorsal aspect. References as in preceding figs.
- Fig. 25. *Hylobates cinereus abbotti*, male juv. Ileo-caecal region from the ventral aspect. Note the fatty character of the dextral mesotyphlon. References as in preceding figs.
- Fig. 26. *Pongo pygmaeus*, adult female. Ventral view of caecum and appendix. References as in preceding figs.
- Fig. 27. *Homo*, female neo-natus. Ileo-caecal region from the ventral aspect showing anomalous arrangement of the meso-appendix and related vessels. *M*, meso-appendix derived from dextral mesotyphlon. Other references as in preceding figs.







*The Morphology and Inter-relationship of the Genera of Syrphid Flies, Recent and Fossil.* By FRANK M. HULL, *University of Mississippi.*

(With 25 figures in the text.)

[Communicated by N. D. Riley, F.Z.S.—Received February 12th, 1948.]

The family Syrphidae comprises a large and attractive group of flies frequently collected by students of insects. There is considerable economic value attached to the aphid-destroying larvae of the subfamily Syrphinae, which contains numerous genera, species and individuals. The Syrphid flies are widely distributed throughout the world and as far as known rivalled or exceeded in number of species only by the Tipulidae, the Tachinidae and perhaps the Asilidae and Tabanidae. Over four thousand and seven hundred species are recognized.\* In addition seventy-two fossil species have been described from the Eocene, Oligocene and the Miocene.

In order to study types of rare genera not available in this country and to arrange for a study of the fossils of the family the author made a visit to several European institutions before the war.† But this study was made possible by the generous loan of material from several institutions, particularly by the extensive collections in the British Museum (Natural History). The collections of the British Museum (Natural History) are especially rich in representatives of genera which are not or seldom found in other collections. Of such scarce genotypes it contains at least sixty-two. Their entire collections contain not less than one hundred and ninety-five genera, or seventy-two per cent., and almost certainly more, of all genera recognized in this study. This may be considered a natural consequence of their material being drawn from many parts of the Dominions. The Recent genera and the phylogeny of the family as a whole are considered in this paper.‡

It is proposed in this study to present a comprehensive review of the Recent genera which will provide workers in widely separated parts of the world with a means of identification of their own fauna as well as a knowledge of the generic fauna of other regions. Another object is an attempt to critically evaluate the characters upon which the subfamilies and genera are based. There appears to be considerable variation in the relative value of the minor categories previously recognized. An effort has been made to illustrate certain genera which have not before been illustrated. In some instances the best description may be inadequate in various particulars (Metcalf, 1937). Finally, as far as it seems possible to do so at this time, this study has sought to apply the concepts of phylogenetics to the history and morphology of the family.

It is appropriate to state here that the index of names is restricted to those which are recognized, together with new or recent instances of synonymy. The long list of older and accepted synonyms and orthographic variations are omitted. The

\* This is the known species total up to June 1st, 1945, exclusive of fossil species.

† This visit was made possible by a grant from the Penrose Fund of the American Philosophical Society.

‡ A review of the fossil genera and species has appeared in the Bulletin of the Museum of Comparative Zoology, Harvard (Hull, 1945).



totals of the species given for each group at the end of its description takes no account of eighteen species described by older authors with the country of origin unknown (*patria ignota*). In Table 3 the totals shown as holarctic are not in addition to the other totals. However, the species totals for the holarctic region in the distribution data given after each description have been included in both the palaearctic and nearctic species totals and must be subtracted to obtain the actual total number of species known for that region. No account has been taken of a few species overlapping in other regions; these have been included in the total for only one region, whichever region seemed most appropriate. Also the bibliography has been greatly restricted to the more important papers. A partial bibliography to Syrphid literature was given by Hull (1936) and Telford (1939).

I am indebted to numerous persons who have generously assisted in these studies. Of the older generation every student of the family must forever be grateful to S. W. Williston, not alone for the compilations, the accurate identifications and careful descriptions, but for his deep insight into the problems of phylogeny. Of the old-world students out of the many who have made signal contributions one may mention Loew, Osten-Sacken, Fallen, Zetterstedt, Wiedemann, especially Meigen and later Verrall. Of the present generation the numerous papers of Curran, Flake, Shannon, Hervé-Bazin, Becker, Brunetti, Collin and Sack have added greatly to our knowledge of this family. Altogether about two hundred persons have published studies upon the Syrphid flies.

I am particularly indebted to Dr. John Smart who extended to me the facilities for the study of this family in the British Museum of Natural History. The collections of the British Museum, drawn as they are from many parts of the world, afford a larger representation of genera and species than are to be found in any other institution. The late Dr. F. W. Edwards was most helpful and Mr. J. E. Collin and Dr. G. D. H. Carpenter also extended courtesies to me. I also wish to thank Dr. F. M. Carpenter, Professor Nathan Banks and Dr. C. T. Brues for much helpful advice and assistance of many kinds. I wish to express appreciation to Dr. C. H. Curran, Dr. E. A. Chapin, Dr. C. L. Fluke and Mr. C. T. Greene. I am also indebted to many others for the courteous reception and the assistance afforded to me at several museums and institutions. Dr. Carpenter and Dr. Fluke have both been good enough to read the manuscript, but for any errors that remain or opinions expressed the author assumes responsibility.

#### THE CHARACTERISTICS OF THE SYRPHID FLIES AND THE QUESTION OF THEIR ORIGIN.

It is not the primary purpose of this paper to treat the question of the origin of the family but it seems to the author that the recessive, or convex, poorly developed face of Microdontinae, Pipizini, etc. point to a common ancestry with the Stratiomyidae, in which family there are already occasional types with a dorsal arista. The spinose scutellum of many species of *Microdon* has, as Curran points out, a suggestive similarity to the Stratiomyids; the same might be said of the occasional thorn-like scutella. There is a possibility that the Syrphids are related to the Bombyliids, but upon the whole this would seem less likely, for the Recent Bombyliids appear more divergent.

Syrphid flies are pilose insects that are often rather large and may range from three to forty millimetres in length. Numerous species are melanic but yet large numbers are bright and gaily coloured. They contain weak fliers as well as strong flying species that hover for long periods and some that emit a pleasing hum. The antennae show two types, the short or elongate antennae with its dorsal arista and the elongate antennae with terminal style. The venation is quite characteristic and in all save a few genera the spurious vein, a major fold, sometimes chitinized, which running between the third and fourth veins and crossing the anterior cross-vein at once distinguishes them as Syrphids. It is obviously improper to exclude *Graptomyza* because it lacks the spurious vein; for it is also absent or virtually so in some *Chrysogaster*, *Psilota* and *Syritta*. These are all, in every other respect, Syrphidae. The student may consult with profit the work of Lundbeck (1916) in his meticulous account of certain features of the Syrphid fly.

#### THE EVOLUTION OF THE SYRPHID FLIES.

In attempting to obtain even a partial view of the development of this family we are handicapped both by the incompleteness of our known record—in spite of its present large size—and our lack of standards of measurement or comparison. These flies range from Greenland and upper Siberia to Patagonia and New Zealand, and to many remote islands of Oceania. Ecologically they range into many habitats but we have no measure of ecological diversion. In order to secure some basis for an understanding of the phyletic history of the Syrphids the author considers the following aspects of these flies: *a.* a consideration of the generalized type of Syrphid, the hypothetical *Protosyrphus*, and its probable features in the light of known fossils as well as the specialized trends of recent forms; *b.* the trends of recent Syrphids in point of changes in structure and form; *c.* the application of the concept of phylogeronts to this family; *d.* the concept of proflorates; *e.* the mimicry within the family; *f.* the basis for a critical evaluation of the minor categories; *g.* the subfamilies of the Syrphidae and their inter-relationship; *h.* the fossil Syrphid flies; *i.* the distribution curve of the species and supra-specific categories; *j.* geographic distribution of Syrphid flies.

##### (a). *The hypothetical Protosyrphus, or generalized Syrphid fly.*

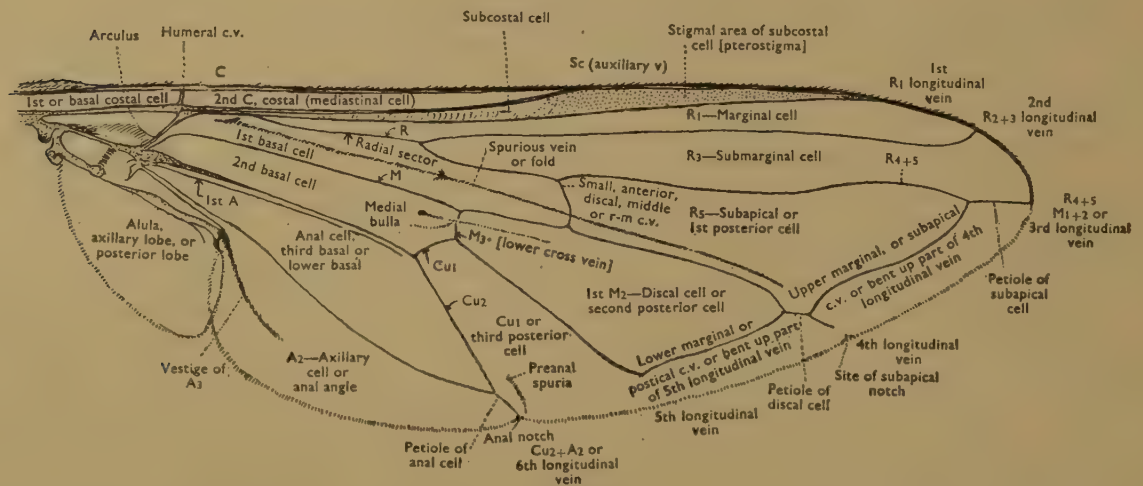
While it is admittedly difficult to trace the origin of this large and successful family, it seems to me that much good may derive from an effort to try to visualize the primitive and generalized type from which the subfamilies may have diverged. Moreover, such an effort helps us to evaluate the recent categories and particularly helps to afford a view of the morphogenesis exhibited in this family.

Morphology. *The head*: if we admit that there is strong tendency towards a produced face in either one of three directions, then I believe we must consider the convex, retreating face, with recessive epistoma as generalized. This is a revision of an earlier view (Hull, 1945) in which the plane face was considered most generalized. It seems likely that the tubercle has been acquired as a specialization. The eyes may be thought of as bare, the upper facets undifferentiated, the males dichoptic. Front moderately developed. Face comparatively wide and pubescent, or bare, without facial stripes. Antennae short, with three segments and with a



dorsal, basal arista. Occiput nearly plane and with a narrow protruding margin. *Thorax*: comparatively flat, without chaetae, the humeri and post-calli but little developed. *Abdomen*: elongate, with nearly parallel sides or narrowly oval, and the margin non-emarginate but not especially rolled. *Legs*: femora simple and slender, without basal setae, both the femora and tibia rounded, without ridges, spines, tubercles, or setae. *Wings*: the wings are moderately large. The third vein is never forked; this is true of not only all recent forms but of all fossil ones dating back to the Eocene; nevertheless this vein may bear a lengthy adventitious branch in certain subfamilies which might be regarded as a remnant of radius five. The adventitious spur seen on the bottom of the loop of some Eristalinae and Cerioidinae may be such a remnant but it seems less likely that it is such a remnant, since in these subfamilies it is usually minute. Fig. 1 shows the more frequent terminology useful in a study of the Syrphid wing and fig. 2 shows certain vein appendages which may be remnants of branches of the radius and medius. The third vein in the derived Syrphids shows a marked tendency towards curvature

Fig. 1.

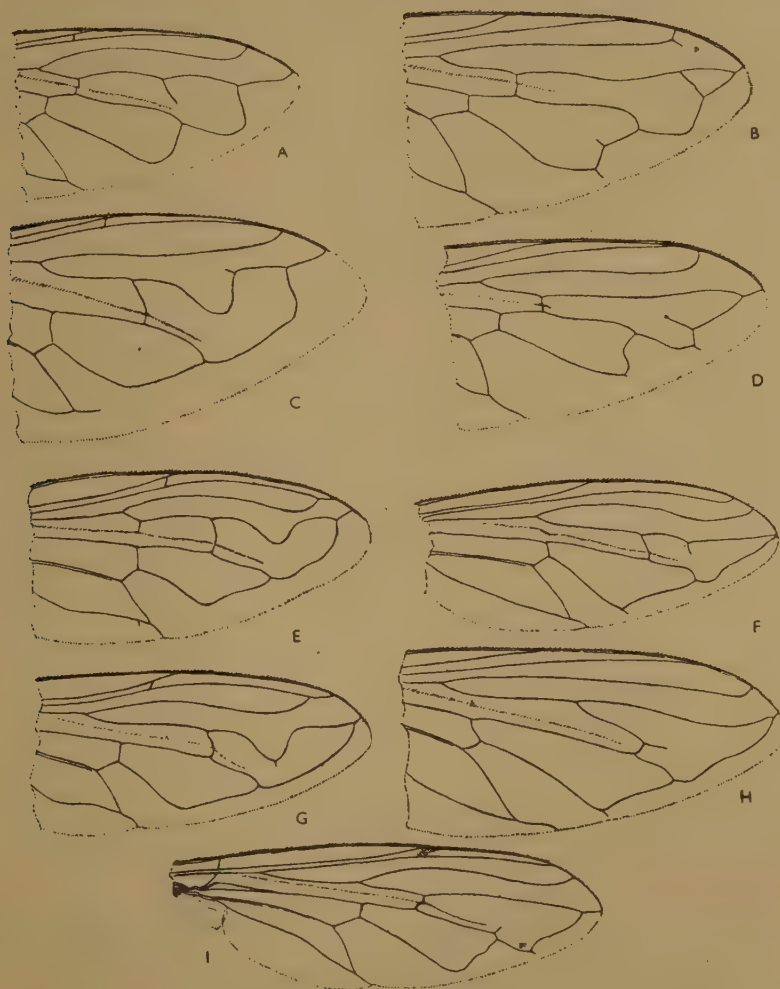


The most frequently used terminologies for the cells, veins and other structures of the generalized Syrphid wing.

and kinking or looping; this may be an expression of a process of strengthening the wing, since it is decidedly more marked in the best poisers and hoverers, the Syrphinae and the Eristalinae, and such flexures are notable in those still more able hoverers, the Bombyliids, in spite of the additional veins they have. In the Syrphidae the recession of the cross-veins and the recession of the apex of the second vein, with its consequent closure of the marginal cell is notable. Recession, as here used, does not necessarily imply that the apex of vein is at the same time recurrent. Primitively then, the Syrphid wing shows a quite widely open marginal cell, a first posterior cell closed in the costa or wing apex as in *Myiolepta* or many Xylotinae; it also shows three posterior cells, the last one of which is open, and two rather long marginal cross-veins, which perhaps represent the bent-up portion of the fourth and fifth veins respectively. The anal cell is always closed. Finally the vena spuria, an inter vein fold, with varying degrees of development and chitinization, represents the outstanding characteristic of the family; this longitu-

dinal fold lying between the third and fourth veins is entirely lacking in a few instances as in *Graptomyza*. In a few cases, as in certain Microdontini, Chrysogastrini, where it appears to be wholly absent, it is nevertheless represented by a slight trough-like curve in the wing surface. In these instances it is uncertain whether the vena spuria has been lost or has never been developed. Fossil Syrphids show the fold quite prominently.

Fig. 2.



Spur-veins or adventitious veins which may represent remnants of branches of the radius or medius such as found in the wings of more generalized Diptera. (All wing patterns and shading omitted.) A. *Microdon barbouri* Hull; B. *Lepidostola calopus* Loew; C. *Merodon* species; D. *Lepidostola similis* Williston; E. *Lycastirrhyncha titillans* Hull; F. *Cerioides rubrobrunnea* Hull; G. *Meromacrus cingulata* Schiner; H. *Stilbosoma cyanea* Philippi; I. *Spheginobaccha dexioides* Hull.

It may be noticed that in the Diptera Brachycera, such as the Stratiomyidae and the Bombyliidae, also great flower frequenters, as well as the Syrphidae, the face is characteristically convex, or at least markedly retreating below. Among the Syrphids the groups with similar face are the Pipizini, Eumerinae, Microdontinae, etc. And apart from the tubercle, the face of most Syrphinae is rather undeveloped



ventrally. Is it possible that these Syrphid groups should be placed lowest among the subfamilies of Syrphidae? The division of subfamilies must have taken place far back, as we find eight and possibly nine subfamilies recognized among the fossil species, four of which date to the Eocene. The two most abundant fossil subfamilies so far as known were the Syrphinae and the Cheilosinae, which latter has twice as many species as the former (and with Pipizini recognized). The greater proportion of Cheilosinae to Syrphinae may not be significant inasmuch as certainly the fossil resin from which they came would be expected to trap greater numbers of Cheilosinae. The author thinks this might follow from the bark-haunting habits of some *Cheilosia*, the feebleness of many Cheilosinae, especially Pipizini, and the infrequency with which resin might be expected to trap powerful flies like *Eristalis* (no amber fossil records known). Brues (1933) has made a remarkable study of the insect components involved in traps, both resin and amber. Of course, other subfamilies may conceivably have been developed at this early time; certainly, of the remaining five subfamilies all are definitely rare as individuals today and may have been equally or more scarce then. The accompanying table analyzes the origin, preservation and composition of the fossil Syrphids.

(b). *The trends of specialization within the family Syrphidae.*

There are several types of alteration of Syrphid flies away from the presumptive generalized type. This matter is rendered more involved because of the complex nature of the insect and its segregation into three well-marked body regions, besides four or five distinct types of appendages and other acquisitions. Morphological alterations might be subdivided into two divisions: first, the changes in the proportionate size, and secondly, changes in type or form. Each of these divisions may then be divided accordingly as they affect the whole of a body region or a subsidiary part such as an appendage or a sense organ. With total size changes or ranges within groups, we are not here concerned.

Wheeler (1928) has commented interestingly upon the presence of the asthenic and pycnic types among insects in general. Such profound changes as may affect all three body regions of the insect simultaneously seem to be more apparent within major categories and no recognition is here found of such types in Syrphid flies. Osborn (1931), however, in commenting upon the types of alteration in single parts of animals (such as Titanotheres) designated a number of distinct patterns of alteration. The responsibility for changes in shape he placed upon what he called groups of alloimetrans; new structures in appearance he called rectigradations. He devised such terms as hypsicephaly, dolichocrany and bathycephaly, and others to represent cranial alterations. Perhaps certain of these terms are suitable for use in descriptive morphology of insects—in particular in Syrphid flies. The changes within most Syrphid genera rest upon the fourth group or type of changes as outlined above, that is, of changes or marked alteration in the form of subsidiary parts.

Chamberlain (1924) suggested an attempt at standardization of genera through limiting the number of their species (and dichotomies). To the author this seems highly artificial. Two other possibilities suggest themselves. One, an analysis of the actual changes in the form and appendages of the major body regions of the organisms; second, a series of categories based upon a decreasing number of

morphological characteristics. In spite of the fact that nature seems to abhor a standardization of its living units, might not something along this line eventually prove possible? There would be no more terms needed than are necessary to describe each of these type of changes as have occurred. Would it not be of value if it served to clarify some of the objectives of taxonomy? Would not such a taxonomic system or method aid in the description of evolutionary change? From the viewpoint of some the only value of taxonomy lies in its use for purposes of identification. However, besides the satisfactions and advantages of a natural classification (Epling, 1939), where that can be achieved, ought not classification perhaps to reflect in some measure the actual diversity within groups? Even though genera be artificial concepts, is it not possible to arrive at some standardization with respect to genera? Epling (1939) refers to species as strands in the evolutionary pattern. But genera are based either on species as monotypic genera, or groups of species as polytypic genera. Therefore genera vary according to the degree of isolation from other bits of the pattern. Two generic complexes may actually be connected. This is the situation Williston (1886) describes. For the Syrphidae this matter is again considered in connection with Fisher's index of diversity for genera and species. In the Tabanidae the vast size of the species aggregates has been frequently urged as a reason for subdivision of this group into many genera, and taxonomists have joyfully proceeded to do so. But because there has been an admittedly great diversification of a group at one level, is it necessary to assume that it has likewise differentiated equally at higher levels? Mayr (1942) has discussed some of the problems connected with genera.

#### *Changes in the form of the head in the Syrphidae.*

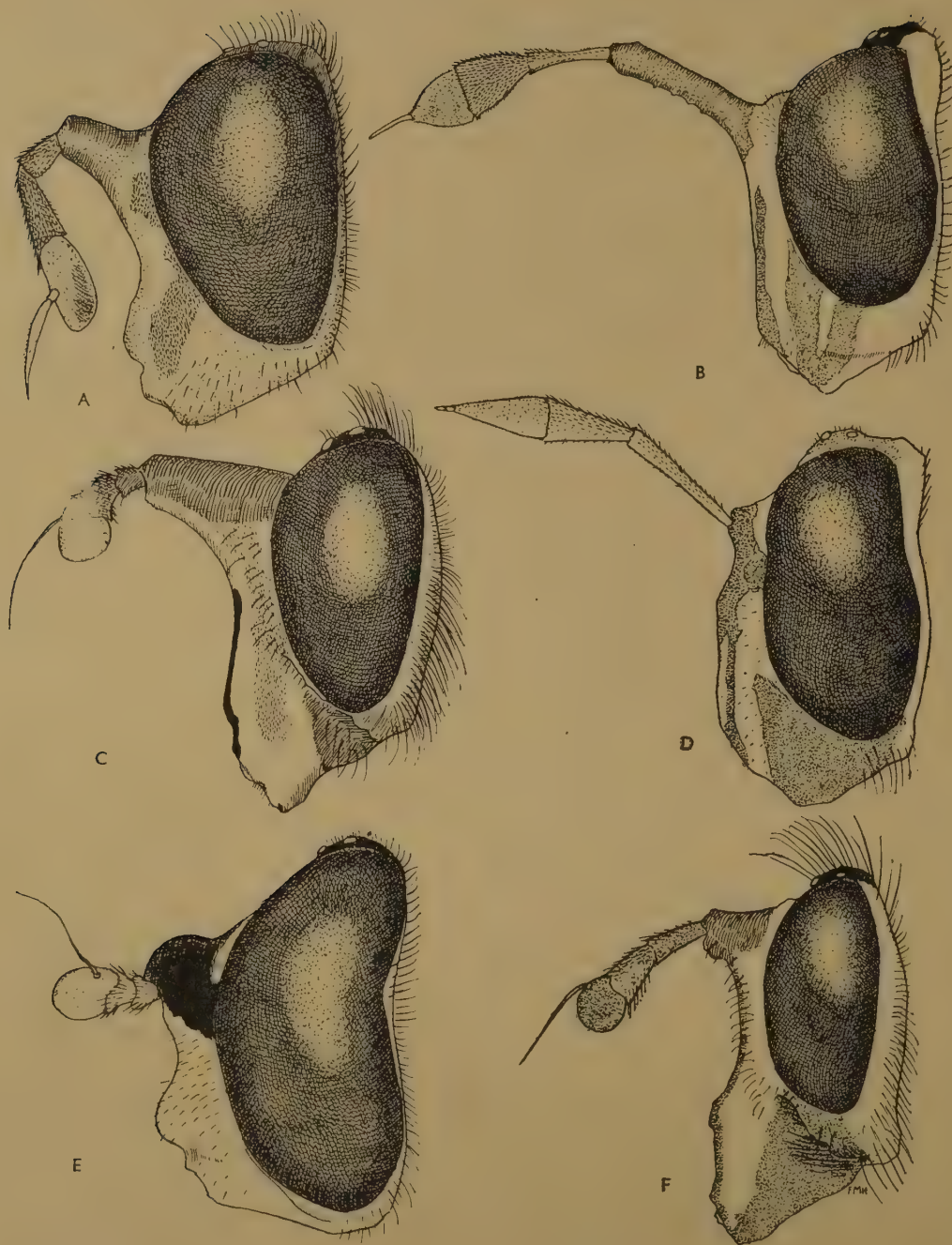
The changes in form of the whole head of insects might perhaps be described in nine types, four of which are referable to the Syrphidae. Brachycephaly, a much shortened head, is seen in *Pseudovolucella*. Sphaerocephaly or a nearly spherical head is found in *Paramicrodon*, *Spheginobaccha*, *Nausigaster* and in three subfamilies. Megacephaly or enlarged head is seen in *Ceriomicrodon*; microcephaly, the head reduced in size, is illustrated by *Pocota*. Other types such as dolichocephaly, or a flattened, pinched head, or optic stalks are not seen in these flies.

(1) There is a tendency on the part of the face and front to inflate (three subfamilies, among which are the genera *Scaeva*, *Styxia*, *Volucella*, *Megaspis*, etc.).

(2) There is a marked tendency on the part of the face to be produced: (a) centrally to form a tubercle (tuberculopsy); (b) downward (conoprosopy), *Conosyrphus*, some *Cheilosia*, some *Volucella*, etc.; (c) diagonally forward, some *Cheilosia*, *Crioprora*, *Eurhimyia*, etc.; (d) forward and porrect (ciconoprosopy), *Rhingia*, *Lycastris*, *Lycastirrhyncha*, etc. Four subfamilies are thus affected. Fig. 3 and other figures show some of the types of face produced in the family. A contrast of figs. 6 and 3 show a shift in the elongation of the face from the lower or epistomal region to the upper or frontal region. The bearers of the former type of face are all nectariphilous or polleniphilous at least, while the latter have diverse habits. Huxley (1932) has discussed growth gradients at some length, with reference, as far as insects are concerned, primarily to the Coleoptera. It does not seem unlikely that the face types in these flies are also reducible to the operation of such gradients controlled and modified by their genes.



Fig. 3.



Convergence of the frontal antennifer in four subfamilies.

- A. *Psarus abdominalis* Fabricius (Psarinae); B. *Monoceromyia tricolor* Loew (Cerioidinae); C. *Somula mississippiensis* Hull, type (Xylotinae); D. *Cerioides minuta* Hull, type (Cerioidinae), antennifer absent; E. *Salpingogaster pygophora* Schiner (Syrphinae); F. *Sphecomyia brevicornis* Osborn (Xylotinae).

(3) There is a tendency for the face, occiput, front and cheeks to reduce (microprosopy) and in consequence for the eyes to appear larger (common—*Xylota*, *Axona*, some Eristalinae, some *Bacchas*, etc.).

(4) There is a tendency for the eyes to reduce (microphthalmia), and face, front, vertex, cheeks and occiput to appear larger in consequence (rare—some *Microdon*, etc.).

(5) There is a tendency on the part of the eyes to acquire pile (thrixophthalmia), *Cheilosia*, *Volucella*, *Pipiza*, etc.

(6) There is a tendency on the part of the eyes to become holoptic and even hyper-holoptic (some Eristalinae). It is to be noted that all subfamilies are predominantly holoptic except the Microdontinae, which are, I believe, without exception dichoptic. Apart from this subfamily there are twenty-six other groups which are widely dichoptic and eleven more which are narrowly dichoptic in whole or in part.\* Four other groups (*Mutillimya*, *Brachyopa*, *Hammerschmidtia* and some *Mesembrius*) have the eyes closely approximated. The majority of all dichoptic groups are in the Eristalinae. Some authors have considered holopticism to be correlated with the aerial habit, and possibly there is good foundation for this idea.

(7) A tendency towards a reduction of the front, and the antennal base or prominence hence raised and the antennae high in profile, *Somula*, *Cerioides*, *Sphecomyia*, etc.

(8) Frontoantennal region produced in three subfamilies; examples are *Somula*, Cerioidinae, *Psarus*, etc.

(9) Face to become quite narrow; scarce, as in some *Baccha*.

(10) Face to acquire pile. The majority of the Syrphidae seem to have acquired facial pile and in most cases extensive pubescence. The pile may be restricted to the facial stripes, or to the antennocular line. Face pilose in part in the subfamilies Syrphinae, Cheilosinae, Xylotinae, Eristalinae, etc.

(11) A tendency of the antennae to elongate (dolichocery). Brachycery or short antennae is the rule, but a few widen dorsoventrally (pelecocery) as in numerous Xylotinae. Elongate antennae seem common and are found in Syrphinae, Microdontinae (where it is the rule but not universal), Cheilosinae, Xylotinae, Chrysotoxinae, Eumerinae, but not Nausigasterinae, Sericomyinae. The third segment

\* The following genera show dichopticism, either widely or narrowly. In *Tuberculanostoma*, *Takaomyia*, *Psarus*, *Habromyia*, *Simioides* and *Brachypalpus* the eyes are moderately to narrowly dichoptic. This is also true of some species but not all species of *Sphecomyia*, *Temnostoma*, *Criorrhina*, *Eumerus* and *Mallota*. Four genera have the eyes very closely approximated in the male; they are *Brachyopa*, *Mutillimya*, *Hammerschmidtia* and *Mesembrius* in part; some species of *Mesembrius* are quite holoptic. Finally there is the group of genera in which the eyes are widely and regularly dichoptic. This group includes all Microdontinae, and in the Eumerinae the genus *Amphoterus*, in the Sericomyinae *Tapetomyia*, in the Volucellinae *Graptomyza* and *Megametapon*, in the Xylotinae *Stilbosoma*, *Merapioidus* and *Crioprora*, in the Cheilosinae *Liogaster*, *Neascia*, *Sphegina*, and *Chalcomyia* and *Hemixylota*, and in the Eristalinae *Helophilus*, *Dissoptera*, *Xenozoon*, *Lycastirrhyncha*, *Lejops*, *Parhelophilus*, *Eurhimyia*, *Aemosyrphus*, *Platynochaetus*, *Lunomyia*, *Dolichogyna*, *Polydontomyia*, *Eristalinus* and *Chasmomma*.

The scarcity of dichopticism in the Syrphinae and its abundance in the Cheilosinae, Xylotinae and Eristalinae will be noted. It may imply a greater antiquity for the Cheilosinae as well as the lines of the Xylotinae and Eristalinae.



may be elongate dorsoventrally, or bifurcate (fissicorny). There have been numerous changes in the arista (pennate, pectinate, glabrous, pubescent, or with thickening or elongation of the basal segments).

(12) A tendency of the arista to move down to the apex of the third segment, all or at least two of the segments of the antennae elongating. This seems to have produced the remarkable antennal type with terminal arista as in Cerioidinae, Calliceratinae. It appears that the condition found in *Ischyroptera* may be an intermediate stage in this process, for here the arista is already fleshy, reduced and terminal, and the third antennal segment seems to be ventrally recessive.

#### *Changes upon the thorax of the Syrphidae.*

(1) There is a tendency towards lobes or tubercles ; some Syrphinae, Volucellinae.

(2) A tendency towards acquisition of chaetae (thoracochaety), only present in some Volucellinae, some Cheilosinae.

(3) A tendency on the part of the metasternum to become pilose. The examination of large numbers of Syrphid flies shows that the metasternum has again and again acquired pile together with its pubescence, which it has sometimes lost, or it may show micropubescence or pollen. Is it possible that pollen precedes pubescence? Few species have pollinose abdomens or mesonota ; *Helophilus*, *Temnostoma* illustrate true pollinosity in contradistinction to micropubescence. The Eristalinae, Cerioidinae, and many of Xylotinae, Cheilosinae and Syrphinae have the metasternum pilose.

#### *Changes upon the abdomen of the Syrphidae.*

(1) A tendency for the abdomen to shorten and widen. Examples : *Eriozona*, *Psilota* (sphaerogastry) ; *Chrysogaster* (platygastry) ; Eristalinae, Volucellinae, etc.

(2) A tendency for the abdomen to become emarginate ; appears to be largely confined to parts of the Syrphinae and perhaps *Chrysogaster*.

(3) A tendency for the abdomen to become slender (dolichogastry), with marked reduction of the abdominal contents, or to become petiolate, the reproductive structures crowded into a compact club-like body. These changes are frequent and are accomplished in several ways. Fig. 4 shows this characteristic within the Cerioidinae.

(4) Reduction in the number of visible segments or segmental asymmetry is rare. The hypopygium, however, tends to enlarge (megapygy) ; *Sphegina*, *Salpingogaster*, *Meromacrus*, *Planes*, etc.

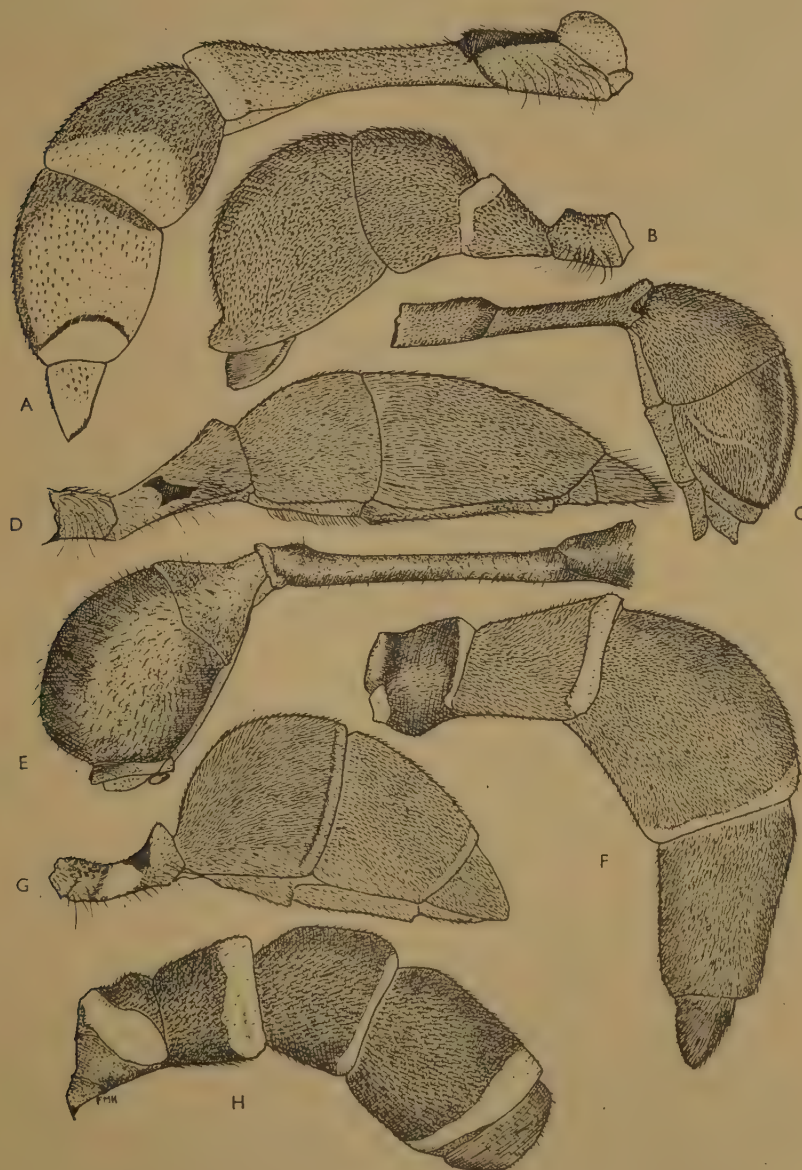
#### *Changes in the legs of the Syrphidae.*

(1) A tendency on the part of the femora, especially the hind pair, to enlarge after several different patterns and to acquire various ornaments of spines, setae or tubercles.

(2) A tendency on the part of the bases of the femora to acquire dense patches of differentiated, short setae, or even spinules. These patches may be delimited by creases or be set off variously from the surrounding pile, sometimes by basal colour. They may consist of long or even curved setae or be reduced to spinules. They appear to be initiated by the anterior femora, spread to the second pair and be present in more than one subfamily upon the hind femora as well ; their emergence

may be foreshadowed by the presence of differentiated pile. After surveying some four or five hundred Syrphids for this character I am convinced that many groups are evolving in this direction; this fact does not entirely eliminate their value in classification. These patches seem absent within the Syrphinae.

Fig. 4.



Trends within the abdomen of the subfamily Cerioidinae.

A. *Monoceromyia gloriosus* Hull, type; B. *Cerioides globigaster* Hull, type; C. *Polybiomyia delicatula* Hull, type; D. *Cerioides braueri* Williston; E. *Ceriathrix bulbosa* de Meijere, type; F. *Tenthredomyia williamsi* Hull, type; G. *Cerioides africana* Hull, type; H. *Tenthredomyia abbreviata* Loew.

(3) To some extent there is a tendency of the basitarsi to differentiate, the hind ones in the Microdontinae, the anterior ones in *Platycheirus*.

There are certain other trends within the legs which will be dealt with in the subfamilies.



*Changes in the wings of the Syrphidae.*

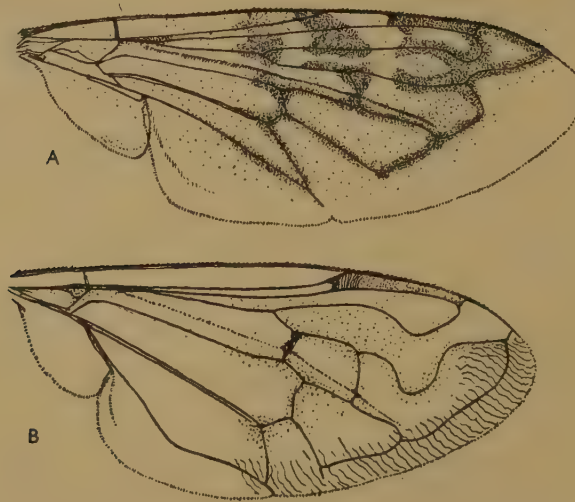
(1) A strong tendency seems to be towards a recession of the apical cross-vein, (Volucellinae, Cheilosinae) and a progression apically of the small cross-vein (Xylotinae). These do not always occur together.

(2) A tendency towards the acquisition of a stigmal cross-vein in which numerous stages may be discovered. Characteristic or common within the Eristalinae, Microdontinae and some Cerioidinae; quite absent in some groups.

(3) A tendency towards the loss of wing villi (three subfamilies, *Scaeva*, some *Syrhitta*, *Megaspis*; seldom complete).

(4) A tendency for the radial sector vein to acquire pronounced bristles or chaetae emerging from the pubescence that usually lines this vein. Lundbeck was of the opinion that these setae occurred in all groups except the Pipizini, but I

Fig. 5.



Convergence of the bulbous apex of the marginal cell and the recessive costa.

A. *Volucella anastasia* Hull, type (Volucellinae); B. *Merodonoides czernyi* Hull, type (Eristalinae).

have not found it so. Verrall believed it a valuable character for the partial characterization of certain groups. It appears to be always present in *Cheilosia*, *Ferdinandea*, *Brachyopa*, Volucellinae, Sericomyinae, Eristalinae in nearly every case, and some but not all Xylotinae. It is apparently absent in Cerioidinae, and most if not all Syrphinae.

(5) A tendency for the third vein to acquire a loop or kink, and for the subapical cross-vein and sometimes the postical cross-vein to become sinuous or deeply sigmoid. Found in five subfamilies (Syrphinae, Sericomyinae, Eristalinae, Cerioidinae, Xylotinae). Other tendencies and conditions such as pattern, closure of marginal cell, the radial sector chaetae and the condition of the sixth vein will be discussed in the subfamilies. (Fig. 5.)

Finally, among general tendencies there is the question of pile and colour. Many Syrphids, especially montane and tundra or even temperate forms, become quite thickly pilose or bumblebee-like. Others like Cerioidinae become relatively bare.

The author inclines to the view that black or melanic species represent the generalized type. It must not be forgotten however that some species marked with pale patterns in part (but elsewhere black) existed as far back as the Eocene, and the existence of the tetramaculate pattern so characteristic of many *Xylota* and *Planes* is beautifully perfected in the fossil *Xylotosyrphus*, which seems to differ but little from our present-day forms except in minor respects upon the wing. Also *Platycheirus*-like patterns were common. With respect to the progressive reduction of black areas, we might point to those yellow extensions from the black colour upon the black species of *Melanostoma* (not all of which are black) to the often quite pale *Platycheirus*, and to the frequent loss of dark pattern in *Mesogramma*.

(c). *The application of the concept of phylogeronts to the family Syrphidae.*

Certain Syrphids appear to show distinctly a phylogerontic condition (figs. 4, 6, 11, 12, 13, 16, etc.). The flies with the very greatly extended porrect snout

Fig. 6.



The development of phylogeronts (and convergence of the porrect epistoma or jutting face) in four subfamilies.

- A. *Lycastirrhyncha willistoni* Bigot (Eristalinae); B. *Rhinoprosopa flavophylla* Hull, type (Syrphinae); C. *Rhinobaccha gracilis* de Meijere (Syrphinae), redrawn from Brunetti; D. *Rhingia nigra* Macquart (Cheilosinae); E. *Lycastis albipes* Walker, type (Xylotinae).



should be placed here, such as *Lycastris*, *Lycastriirrhyncha*, *Rhingia*, even though, as in *Lycastris*, the slender labellum is not yet as long as in *Megistorhynchus* or some Pangoninae. The marked and interesting development of this snout places these Syrphids in a class by themselves. Moreover, there are the hyper-vesiculous types such as the bituberculate *Cyphipelta* and the odd *Alipumilio*, which latter seems to have moved towards several extremes. Perhaps *Axona* with its hyper-holopticism and inflated abdomen belong here, and perhaps also *Tachinosyrphus* with its plethora of chaetae and bloated face. It might be argued that forms like *Ceriomicrodon*, with overgrown head, reduced and filopetiolate abdomen, and *Pelecinobaccha*, or *Baccha fillissima*, belong to the class of phylogeronts, having largely reached the end of their development. *Nepenthosyrphus* with its shortened, stubby, much reduced abdomen and massive hind femora surely belongs here. Among the Cerioidinae, *Stipogaster* seems to have gone far in its development.

Of the face and abdomen above discussed, some of the changes in the form are illustrated in the plates.

(d). *The concept of proflorates.*

By this the author refers to those major genera about which centre numerous subgenera or lesser categories, and which give all the appearance of actively flowering out into many minor morphological types within or near Recent time. These are those groups, in short, in which morphogenesis seems particularly apparent. By this term the author has in mind the active genera with regard to comparatively Recent time. In the Syrphinae we can point to *Baccha* with its subgenera *Mimocalla*, *Pelecinobaccha*, *Calostigma*, *Styxia*, *Therantha*, etc.; to *Metasyrphus* with its *Didea*, *Dideoides*, *Asiodidea* and *Scaeva*; to *Epistrophe* with its *Metepistrophe*, *Fazia*, *Claraplumula*, *Allograptia*, *Spaerophoria*; *Melanostoma* with its *Tuberculanostoma* (possibly not a forward development), *Platycheirus*, *Pyrophoena*, *Spathiogaster*, *Carposcalis*. But not the 130 species of *Mesogramma* in which there seems to be very little development taking place other than in pattern. In the Microdontinae we can point to *Microdon* with its *Serichlamys*, *Eumicrodon*, *Myiacerapis*, *Ptilobactrum* (which, odd though it is, differs in only one anatomical feature), *Chrysidimys*, etc. In *Volucella* we may point to the host of minor categories, beginning with *Phalacromyia*, *Ornidia*, *Volosyrpha*, *Volucellosia*, *Lepidopsis*. Nowhere is the concept seen to better advantage than in the Eristalinae where we may remark *Mallota* with at least eight minor groups associated; perhaps the stem function should be assigned to *Arctosyrphus*, which to the author seems more generalized; it is no argument against *Arctosyrphus* that there is only one species known of it, and twenty or more of *Mallota*. The *Plagiocera* stem has produced, or at least includes, *Quichuana*, *Habromyia*, *Myiatropa*. Finally associated with *Eristalis*, in which *Pseudoeristalis* or *Eristalinus* seems to be the generalized type, there will be noticed this cluster of minor groups, *Kertezomyia*, *Solenaspis*, *Eristalinus*, *Eristalomyia*, *Merodonoides*, *Lathyrophthalmus*, *Eristalodes*, *Velocimyia*, *Helophilina*, etc.

(e). *The mimicry within the family Syrphidae.*

The mimetic lines within the family seem to be numerous and are most fascinating. The type of mimicry falls within that known as Batesian; presumably there is a

gain to the flies inasmuch as they mimic the well defended Hymenoptera. As to the practical return to the insect, so keen appears to be the competition among insects with their numerous enemies, who will say that even a very small number of individuals saved by mimicry might not have an ultimate value to the species? There are several mimetic types. In the Syrphinae there are the bright coloured wasp-like *Doros* and *Salpingogaster*; the Xylotinae with *Sphecomyia*, *Temnostoma*; *Spilomyia* furnish some exquisite types, and we have the *Bombus* types, even to red terminal segments of the abdomen, in some species of *Eristalis*, *Mallota* and Volucellinae. The Microdontinae are remarkable for *Myiacerapis*, the bee mimic, *Pseudomicrodon* and *Mixogaster*, the wasp mimics. In *Mixogaster sartocryptus* the metanotum is much developed and slanting as so often seen in wasps. The brown anterior border of the wing is well known; why else should it be there except for effective purpose of mimicry? *Ubristes* seems to copy the Trigonid bees; *Chysidimyia* can scarcely be told experimentally among Chysidids. *Mutillimyia* seems to copy the Mutillid wasps. *Graptomyza* mimics the Meliponid bees. But it is among the Cerioidinae that the mimics cluster. Here we find several types of wasps faithfully copied in as many as six or eight particulars, not least remarkable being the wing fold along the sixth vein in *Polybiomyia*. Herein is a possibility of Dixey's (1908) reciprocal mimicry or mimetic attraction. The whole general field of mimicry and the studies which support or do not support the theory have been well summarized by Pearse (1939). Finally it should be noted that *Xylotomina chalybea* copies our blue-black mud-dauber wasps, even to the nervous twitching of the wings. A captive specimen of *chalybea* goes about twitching its wings at a rate of approximately twenty to fifty or more times per minute. The habit of both Hymenoptera and Syrphids frequenting the flowering shrubs might conceivably place a valuation upon similarity in appearance.

(f). *The basis for a critical evaluation of minor categories.*

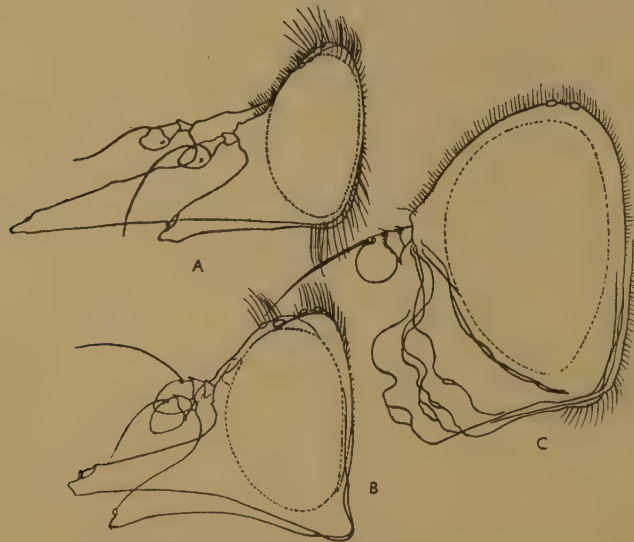
The evaluation of the minor subdivisions of this family is beset with numerous difficulties. If the student will go to the trouble to construct a tentative phylogenetic diagram of relationships within the several subfamilies the determination of the more obvious genera becomes more or less apparent. However, mere size in terms of numbers of species cannot be always argued as a measure of generic status. Even a species group may wax large it would seem, as a result of, let us say, an ebullience of rapid morphogenesis, without assuming or making radical progress structurally. It is, however, helpful in instances to arrange the groups downward in terms of numbers of species, and where this is done it is often possible to obtain further information upon the relative importance of a group. Data of value may be obtained by mapping the distribution of the species of so-called genera or subgenera. Consequently in each subfamily one may segregate these marked types, which I have termed remote genera, as for example *Nepenthosyrphus* in the Xylotinae. Then we may contrast that type of category which is based upon an extension of some existing forms, rather than a new and diametrically opposed type. An example would be the contrast between *Stipomorpha fraudator* Shannon with its flared base and pinched, pipe-like terminal half of the abdomen, and



*Ceriomicrodon petiolatus* Hull in which the basal half of the abdomen is quite slender and petiolate and the apex of the abdomen is club-like. Finally there is the question of the numerous convergences and parallel developments of characters that have appeared in so many subfamilies. A few of these are shown in figs. 3-6. If we have to rely upon such characters, as for instance metasternal pile, to substantiate genera, it seems we are placing genera upon very slender bases, no matter how many species are involved.

The author suggests that for many polytypic genera it is possible to select a species which for the known discovered species represents the most generalized of the species of that genus. This might be designated the eotype of that genus. Correspondingly there might be some species within the genus which have changed morphologically to a marked degree and represent for known species the farthest development of this genus. Such a species might be called the prosotype (the

Fig. 7.



Superimposed profiles of different species of Syrphids, within three genera, showing the variable extent to which certain trends of development have proceeded.

A. *Lycastris cornutus* Enderlein and *Lycastris albipes* Walker ; B. *Rhingia* species ; C. *Cheilosia* species.

advancing type). Examples will be seen in fig. 8 E-F (*Mesogramma* and of fig. 9 C-D (*Rhinoprosopa*). Where the elongation has not even begun in the eotype, as in figure 10 D (*Melanostoma*), it is perhaps proper to designate the prosotype (fig. 10 c) with a special name ; this has indeed been done ; Enderlein recently gave the name *Carposcalis* to this type. The author has segregated the eotypes of the genus *Graptomyza* under the name *Protograptomyza*.

Fig. 7 shows the varying extent of a trend of development between different species within a genus.

Pattern or style of marking is thought of, and I believe usually rightly, as the poorest possible basis for the making of genera ; it is for this reason that the author has to some extent devalued such groups as *Allograpta*, which have a very distinctive pattern, or *Xanthogramma* with its yellow thoracic stripes. The neotropical *Allograpta* as well as these *Epistrophe* (*Metepistrophe*), have the face developing

into a prominent peak, but each seems to retain its characteristic pattern. Is the structural change of the face here to be subordinated to pattern? Presumably any character may vary in importance, and a trivial character possessed by few species today may include all or most of the species of the group at some future time.

I have, therefore, represented each subfamily in the following terms; the genera I divide into tribogenera, remote genera (isolated genera without close relatives, yet not phylogeront), proflorates (very active genera), and phylogeronts and the unpeculiarized genera that remain. It is this latter body largely, and especially the proflorates, which are further divisible into subgenera. In brief the following characters have been considered of no greater value, at the most, than of subgeneric status: ocular pile, all minor differences when alone, metasternal pile, etc. It should be realized that there are a host of minor structural differences such as the form of the ocellar triangle, its elevation, the occipital indentation, the flattening of the pile here, its reduction there, a curve in a vein here, the presence of facial pile, or its absence, etc. The list might be multiplied almost endlessly. No good purpose is served by giving names to all these permutations, and it is to be hoped that the tendency to do so will be discouraged.

It is absolutely essential to recognize subgenera in order to preserve any possible semblance of values. Accordingly I have attempted to indicate what seems to me to be those genera heretofore erected which should be thought of as subgenera. It is fruitless to say they should be abolished, for unfortunately the tendency is in the other direction (Brues, 1929). It is only by drawing upon all available data from fossils, distribution and species abundance that a sense of values can be preserved, and I have attempted to use data of this type in an effort to set values upon the names that have heretofore been proposed. This study will seem well worth while if a start is made towards placing the arrangement of the family upon a better basis and if the keys and illustrations and description briefs are of assistance to new students in the study of this large family. The author does not recognize colour characters and patternal types as basis for separation of category higher than a species group. It is to be hoped that the students of this family will by common consent refrain at this point from giving names to colour and pattern groups.

(g). *The subfamilies of the Syrphidae and their inter-relationships.*

Numerous difficulties arise in the matter of segregating these flies into subfamilies. Much of this seems to be due to what might be called a combination of convergence and orthogenetic morphogenesis. There is a tendency for the subfamilies to progress in a common way. For instance the following characters seem to arise or appear in several subfamilies: (1) the metasternum becomes pilose; (2) the base of the hind femora becomes beset with spinules or setae; (3) there is a tendency for the stigmal cross-vein to appear; (4) there is a tendency for the hind femora to become knife-edged upon its basal third or fourth, with or without serrulations or setae; (5) there is a tendency for a loop to form in the third vein; (6) there is a tendency for long bristles to appear upon the radial sector. These are only a portion of the characters which tend to appear. To illustrate the overlapping involved in these types of characters it may be pointed out that out of fifty species of *Volucella* checked, the stigmal cross-vein has not appeared in thirty-seven, but in twelve it is



possible to recognize a trace or beginning stages of it, and it is definitely present in *Volucella taiwana*. Again, in the Eristalinae a large proportion have the hind tibia knife-edged, and others show it just beginning; the same situation holds in the Xylotinae with it present in a rather smaller proportion of cases. It was once thought that the Eristalinae were the only flies in which basal patches of femoral setae are found on the third pair of legs; this is not true and they are present upon all three pairs of legs occasionally in several non-Eristalinae genera. The position of the small cross-vein was once regarded as an infallible means of segregation of the subfamilies. It now seems evident that while still, in the main, we may use it for the segregation of some groups, there are exceptions which must be taken into consideration. Possibly, if we could always distinguish the convergent orthogenetic characters from the true divergent characters we should be able to perfect the classification of the Syrphids even though connectant forms still persist. Somewhere about each type it would seem there should be some character which should furnish a clue to its past history. However, it appears likely that there may be no real, tangible basis of separation between some of the subfamilies, such as for instance the Cheilosinae and the Xylotinae, that separation must remain arbitrary and a matter of convenience, and that the only real distinctions between these subfamilies lie in the realm of the intangibles such as the brevity of the pile and the more elongate form of most Xylotinae. In each subfamily then, the basic position must be given to that group which most nearly meets the theoretical generalized type, not excluding such characteristics as shape, colour and pile. It may be that we have still much to learn about the more obscure or index characters of the family. Some progress has been made by students in the past, as when it was discovered that the Syrphinae may be segregated from the residuum of the family through the bare or practically bare humeri. Again, flies like the Cerioidinae and the Calliceratinae are easily segregated. It must not be overlooked that the relative value of a character for real purposes of classification varies from group to group and the trivial variation of one time may a long time later have come to separate great numbers of species or groups. For instance the emarginate scutellum is characteristic of many Eristalinae but occurs rather sparingly in other subfamilies. Again, in Tabanids so simple a thing as the presence or absence of tibial spurs separate large groups.

It seems beyond dispute that those groups with the small cross-vein at the middle or well beyond the middle of the discal cell represent the most specialized of the Syrphidae. This would include the Eristalinae, Psarinae, Cerioidinae and Xylotinae. In all of these the migrant tendency of the cross-vein is quite marked. The first or principal divergence of the family, I believe, arises over the development of the lower face. This would leave the Microdontinae and Eumerinae and possibly the Nausigasterinae off in a group by themselves, with undeveloped face and other associated peculiarities. The second divergence would involve the removal of the Syrphinae and Chrysotoxinae and it is possible that these should be combined. The third main divergence would involve the tendency of the small cross-veins to move to or beyond the middle of the discal cell. This leaves the Volucellinae with their close allies the Sericomyninae together with the Cheilosinae which also have the Pelecoceratinae and Calliceratinae for further associates. The

relative number of species and the regional distribution of the forms throw some interesting light upon the comparative development of the subfamilies. Table 1 gives the numbers of each category by subfamily.

TABLE 1.—The Relative Development and Homogeneity of the Several Subfamilies.

	Cheilosinae.	Xylotinae.	Syrphinae.	Eristalinae.	Volucellinae.	Sericomyiinae.	Microdontinae.	Nausigasterinae.	Eumerinae.	Chrysotoxinae.	Pelecoceratinae.	Ceriodinae.	Psarinae.	Calliceratinae.
Number of species . . .	822	481	1254	827	374	43	340	14	150	87	20	176	2	17
Number of subgenera . .	9	14	13	23	2	2	19	—	3	—	—	2	—	—
Number of genera . . . .	9	21	11	25	1	2	3	1	1	2	3	4	2	1
Number of tribogenera .	6	6	2	2	2	1	2	—	1	—	1	1	—	—
Number of remote genera . . . . .	2	6	4	2	1	—	2	—	—	—	—	—	—	—
Number of phylogeront genera . . . . .	2	2	1	2	1	—	1	—	—	—	—	—	—	—
Number of genera over 100 spp. . . . .	1	1	4	2	1	—	1	—	1	—	—	—	—	—
Number of genera over 50 spp. . . . .	3	3	8	4	2	—	1	—	1	1	—	2	—	—
Number of genera over 25 spp. . . . .	7	6	13	8	3	—	1	—	1	1	—	3	—	—
Number of genera over 12 spp. . . . .	15	12	16	11	3	1	2	—	1	1	1	4	—	1
Number of fossil species	41	2	19	6	1	—	—	—	2	1	—	—	—	—
Number of fossil groups (not included above).	18	2	5	4	1	—	—	—	2	—	—	—	—	—

(h). *The fossil flies of the family Syrphidae.*

Table 2 presents in condensed form our present knowledge of the fossil Syrphid flies. The author (1945) added thirty-nine species to the known fossil Syrphids, bringing the number known to seventy-two. While seven or eight subfamilies are recognizable from these flies the great majority fall into the Cheilosinae and Syrphinae. Serres (1829) believed that he had recognized *Microdon* from the Oligocene. The author conceives of those flies with the retreating, undeveloped face as the lowest and most generalized in the family. This would include the Microdontinae which are quite specialized in their larval habits, even though it may not have been an originally difficult acquisition. The Syrphinae too are characterized by a rather specialized larval habit, since they are aphid predators. Presumably the early larval habit of this family would be that of living in decaying organic matter, much as do the Stratiomyidae and their allies. Among the Syrphidae we find many Cheilosinae whose larvae apparently do subsist upon



organic matter and plant detritus. The known fossil Syrphids show that four subfamilies had differentiated by Eocene times and so the first divergence within the family may well have been much earlier. We cannot of course be sure what

TABLE 2.—The Distribution of Fossil Syrphids by Horizon, Generic and Subfamily Assignment and type of Preservation.\*

	Syrphinae.	Chrysotoxinae.	Cheilosinae.	Eumerinae.	Eristalinae.	Volucellinae.	Xylotinae.	Totals.
Total number of species.....	19	1	41	2	6	1	2	72
Total number of genera .....	4	1	17	2	4	1	2	31
Total number of subgenera .....	—	—	1	—	—	—	—	1
Total species from amber .....	1	—	27	2	—	1	1	32
Total species from non-amber deposits .....	18	1	14	—	6	—	1	40
Total species from Miocene .....	12	1	9	—	1	—	—	23
Total species from Oligocene .....	3	—	30	2	3	1	1	40
Total species from Eocene.....	4	—	2	—	2	—	1	9
Total from Recent genera .....	19	—	21	—	5	—	—	45
Total species from Recent subgenera .....	—	—	—	—	—	—	—	—
Total species from Extinct genera .....	—	1	18	2	1	1	2	25
Total species from Extinct subgenera .....	—	—	2	—	—	—	—	2
Total number of Extinct genera .....	—	1	11	2	1	1	2	18
Total number of Extinct subgenera .....	—	—	1	—	—	—	—	1
Total number of Recent genera .....	4	—	6	—	3	—	—	13
Total number of Recent subgenera .....	—	—	—	—	—	—	—	—

\* Only valid species to which specific names have been given are included in this table.

may have been the larval habit of the earliest members of the Syrphinae. It may well be that the earliest of all Syrphid flies were generalized members of the Cheilosinae with recessive and non-tuberculate face.

(i). *The distribution data of the family Syrphidae.*

A number of students of taxonomic problems have attempted to find some method of submitting the taxonomic arrangement of various groups of organisms to mensuration. Chamberlain (1924) devised what he called the hollow curve of distribution of the large genera and small or monotypic genera. It is at once apparent that there are many monotypic genera in a given family but fewer ditypic, and still fewer tritypic genera. Fisher, Williams and Corbet (1943) have made a recent study of the distributions of genera by size within larger categories. They arrive at the conclusion that such distributional data, instead of representing a hyperbolic series as once thought, is really a convergent logarithmic series. The author has, with the assistance of mathematical colleagues, Dr. A. B. Lewis and Dr. G. W. Nicholson, at the University of Mississippi, attempted to apply this data to the present arrangement of the genera and subgenera of the Syrphids. That

there are interesting general relationships that may hold within certain limits can scarcely be doubted. Inspection of Table 1, of the numbers of genera with species totals above 100, of those above 50, those above 25, etc., show a remarkable regularity. The author in this study recognizes 270 genera, subgenera and infra-

TABLE 3.—The Distribution of Syrphids by World Regions.\*

Subfamilies.		Cheilosinae.	Xylotinae.	Syrphinae.	Eristalinae.	Volucellinae.	Sericomyiinae.	Microdontinae.	Nausigasterinae.	Eumerinae.	Chrysotoxinae.	Pelecoceratinae.	Ceriodinae.	Psarinae.	Calliceratinae.	Totals.
Palearctic	genera species	18 285	13 80	22 227	22 195	1 19	4 14	1 16	— —	1 60	1 26	3 16	4 17	1 1	1 9	965
Nearctic	genera species	21 311	21 160	20 239	10 95	3 32	4 16	3 43	1 8	— —	1 22	2 3	4 21	— —	1 3	933
Holarctic	genera species	2 2	6 6	10 36	4 9	1 1	1 1	— —	— —	— —	1 1	— —	— —	— —	— —	(56)
Neotropical	genera species	17 73	21 78	23 535	14 186	11 265	1 1	14 153	1 6	— —	1 2	— —	4 47	— —	1 1	1367
Ethiopian	genera species	3 25	5 27	10 71	20 142	1 9	— —	5 34	— —	3 35	1 1	— —	4 28	— —	— —	372
Oriental	genera species	12 106	12 116	18 141	25 178	2 52	4 12	9 75	— —	3 45	1 36	1 1	5 42	— —	1 4	808
Australian	genera species	5 21	8 18	6 35	8 28	1 5	— —	3 18	— —	1 7	— —	— —	3 18	1 1	— —	151
Oceania	genera species	1 1	1 2	4 6	3 3	1 1	— —	1 1	— —	1 3	— —	— —	2 3	— —	— —	20
Total genera Total species		77 822	81 481	103 1254	104 827	20 383	13 43	26 340	2 14	9 150	5 87	6 20	26 176	1 1	4 17	4616

\* The totals for the nearctic include all species north of Mexico and all holarctic species; the palaeartic totals also include the holarctic totals. The totals for the neotropics include all species south of the United States; the Australian totals include only Australia, Tasmania and New Zealand, and close-by islands; Oceania includes Fiji, Samoa, Tahiti, New Hebrides, Hawaii and Polynesia, Melanesia in general.

genera. Ninety-five of these are monotypic, twenty-six are ditypic; the first twelve elements in the series runs as follows—95, 26, 18, 13, 10, 8, 2, 4, 4, 1, 2, 6 with, at the end of the series, two genera with each 300 species. He has also prepared three other schema representing a modified contraction of groups (that is,



a reduction or fusion of the number of groups), and again a full or what to the author appears to be a maximum contraction, and finally a schema in which the groups are expanded to a total of 283—recognizing virtually all names ever proposed. Each of these has been tested upon the basis of Fisher's theory. None of these four arrangements results in a perfect fit of the calculated data (based upon 4,720 species for each case, and of generic totals of 168, 186, 270 and 283 respectively). However, the scheme adopted in this paper may, apart from the large number of monotypic groups, perhaps be regarded as a reasonably close approximation to the calculated data. Thus with the series already given for the first twelve terms of observed data, the first ten calculated terms are as follows: 61.6 monotypic groups, 29.6 ditypic groups, 19.5 tritypic groups, 14.4 tetratypic groups; and continued: 11.4, 9.4, 7.9, 6.8, 6.0, 5.3. There are observed to be 181 groups, with ten species or less against a calculated number of 171.9 such groups.

It can hardly be expected that the results of observation and calculation will agree as closely for all groups as they have for some groups. From the above data it might be argued either that we have gone too far in recognizing monotypic groups; or that the very large genera of the Eristalinae, Syrphinae and Cheilosinae should be further subdivided. Neither of these conclusions are legitimate inferences until the application of the theory has been much more widely tested.

(j). *The geographic distribution of the family Syrphidae.*

The geographic distribution of the Syrphidae presents numerous interesting relationships. Table 3 gives an approximate survey of the species and genera (generic totals above, species totals below) for each of the world regions by subfamilies. The abundance of this family in the neotropics is interesting but there is good reason to believe that for certain other regions, such as the oriental and Ethiopian, collections and studies are incomplete. The number of species from the nearctic and palaearctic regions is approximately the same.

There are fifty-six species of holarctic Syrphids, excluding introduced species. It does not seem to the author that the generalizations formerly laid down concerning the greater relation of our eastern Syrphids to Europe than our western ones any longer holds good. There are perhaps a dozen species occurring on Greenland, most of them nearctic. The species from Oceania are comparatively few. The author (1937) listed the species from this region and one or two have since been added. From Australia and Oceania there are six; from Malaysia or New Guinea and Oceania there are four; from New Zealand and Oceania two; from Oceania alone, endemic, ten. Thus the total which arises or ranges into Oceania is twenty-two. There are numerous species from New Zealand. Species range as far as Hawaii and Christmas Island.

*A key to the subfamilies of the Syrphidae.*

1. The face completely recessive, usually convex with the mouth small; tubercle never present; face always retreating and undeveloped at the epistoma; occiput often thick and tumid and well developed. Metasternum always pilose; femoral base setae always present at the base of the first, usually the second and sometimes the third pair of legs. Weak flying, ground-frequenting species ..... 2

The lower face is well developed and often quite prominent. The face frequently bears a conspicuous tubercle. Metasternum pilose or bare. Femoral setae present or absent..... 3

2. Stigmal cross-vein present with rare exceptions. Antennae almost always elongate, particularly the first and third segments. Face convex or rarely straight. Apical and postical cross-veins strongly recurrent, seldom angulate and spurred. Third vein usually with a branch vein, possibly representing the 5th radius. Hind femora always with a subbasal, their tibiae with a subdistal cicatrix; these scars sometimes prominent. Hind tibiae rounded. Eyes almost never pilose; males dichoptic.....

MICRODONTINAE.

Stigmal cross-vein almost never present. Antennae almost always short, the second or third segments rarely elongated. Face retreating or slightly convex. Apical cross-vein moderately recurrent and usually with a distal angle and spur; third vein never with spur. Hind femora and tibiae without cicatrices, their tibiae usually compressed basally to a non-setate knife-edge. Eyes usually pilose; males holoptic or dichoptic.....

EUMERINAE.

3. Humeri wholly destitute of pile or with a few hairs along the posterior margin. The femoral bases without setae, the base of tibiae rounded, the femora simple. Anterior cross-vein always before the middle of the discal cell... 4

Humeri pilose, femoral setae often present, the femora frequently enlarged or the tibiae modified. Anterior cross-vein either basal or distal in position. 5

4. Antennae quite elongate, the abdomen convex and emarginate..... CHYSOTOXINAE.  
Antennae short or if elongate the abdomen is not convex and emarginate .. SYRPHINAE.

5. Surface deeply punctate; face with a tubercle, the subtubercular portion short and retreating; abdomen subcylindrical, the elongate fourth segment characteristically turned down apically as well as externally enclosing and concealing the remainder. Third vein and apical cross-vein sinuous. Anterior cross-vein basal in position. Antennae always short.....

NAUSIGASTERINAE.

Not deeply punctate flies with cylindrical abdomen and case-like fourth segment..... 6

6. Anterior cross-vein basal with rare exceptions; stigmal cross-vein usually absent..... 7

The anterior cross-vein has migrated to where it usually is beyond the middle of the discal cell; stigmal cross-vein usually present..... 11

7. Antennae elongate, with a true terminal style..... CALLICERATINAE.  
Arista characteristically dorsal; if terminal the third segment is flattened and pendulous below and the arista thickened and elongate..... 8

8. The arista arises terminally or beyond the middle of the third antennal segment; arista oftentimes tumid.....

PELECOCERATINAE.

The arista is basal and slender..... 9

9. Apical cross-vein strongly recessive, the costa and the end of the third vein usually quite recessive. Antennal arista with rare exceptions plumose; metasternum always pilose; femora simple, the base of the hind tibiae rounded. The face tends to be produced downwards or rarely diagonally downward; face with usually a tubercle. Radial sector always with bristles..... 10

Antennal arista rarely plumose and if plumose neither the apical cross-vein nor the costa are recessive. Anterior cross-vein usually well before the middle of the discal cell, rarely or never beyond it. Radial sector bristles, facial tubercle and metasternal pile sometimes absent. Femoral setae usually present upon the first femora, sometimes upon all the femora....

CHEILOSINAE.



10. The apical cross-vein is strongly recessive, the costa and the end of the third vein usually quite recessive. Sixth vein straight or concave on its posterior side. Third vein never with a loop. Anterior cross-vein always well before the middle of the discal cell ..... VOLUCCELLINAE.  
 Apical cross-vein only moderately recessive, the costa but little or not at all recessive. Face often deeply produced. Sixth vein always bent and concave on its anterior side. Anterior cross-vein at or just before the middle of the discal cell. Third vein sometimes with a deep loop ..... SERICOMYINAE.  
 11. Antennae elongate and with a true terminal style ..... CERIOIDINAE.  
 Antennae never with a terminal style ..... 12  
 12. The antennae are elongate, the thick and fleshy arista arises at or beyond the middle of the third antennal segment. Front greatly produced into an antennifer. Face well developed below. Anterior cross-vein slightly before the middle of the discal cell and quite transverse ..... PSARINAE.  
 The arista arises near the base of the third antennal segment and always before the middle; usually slender and rarely thickened ..... 13  
 13. All three pairs of femora with well-developed basal patches of setae; metasternum always pilose; third vein always with a loop; sixth vein strongly bent, the anterior side concave. Radial sector bristles usually present. Hind tibia usually with a knife-edge ..... ERISTALINAE.  
 Only the first or second pairs of femora with femoral setae; metasternum with or without pile; third vein usually without a loop though characteristically sinuous. Radial sector bristles occasionally present. Hind tibiae often with a knife-edge upon the basal third ..... XYLOTINAE.

#### THE SUBFAMILY SYRPHINAE.

This is a large subfamily for which about fifty groups have been proposed, omitting names definitely equivalent and in synonymy. There are few large flies in this subfamily and the great majority are medium sized and brightly coloured with a preponderance of yellow or orange or yellowish brown. Almost exactly thirty per cent. of the described species fall here. The subfamily is based upon the following three distinctions: (a) the humeri and the area between is bare and without pile, although in some instances there may be a few hairs upon the posterior edge of the humeri; (b) the arista is dorsal; (c) the anterior cross-vein is placed well before the middle of the discal cell; (d) the femora are simple, with no basal patches of setae; the hind tibiae are, with two exceptions, always straight, slender, simple, their ends transverse. There is never a stigmal cross-vein or trace of one, nor are there radial sector bristles present. The principal trend seems to be towards the emarginate abdomen as in the Syrphini. This leaves a large group, the Epistrophini, with the edges of the abdomen rolled. The great group of which *Baccha* is a centre is confusing, as many of them are distinctly emarginate upon the terminal segments. I am inclined to believe that these are separately related to the Epistrophini and are independently acquiring an emarginate abdomen. It may be that the present mass of species of *Baccha* represent two unrelated groups. The same difficulty presents itself with *Mesogramma*. There seems no reason to doubt that many of the subdivisions in this subfamily rest upon slender grounds and colour distinctions have occasionally been involved. *Cyphipelta* is a remote genus and easily removed. The most specialized forms are perhaps *Dideoides* or *Rhinobaccha*. *Paragus* is peculiar in that its species show both emarginate and non-

emarginate types, both metasternal pilose and pubescent types; it may be regarded as transitional; it is perhaps the smallest Syrphid fly.

After attempting to trace the phyletic relationship and weighing the structural differences the author recognizes the following categories: two tribogenera, one phylogeront genus, eleven genera besides twenty-eight subgenera. Of these subgenera those with least adequate basis are: *Pyrophæna*, *Olbiosyrphus*, *Toxomerus*, *Didea*, *Asiodidea*, *Spathiogaster*, *Mimocalla*, *Ischiodon*, *Eupeodes*, *Allograptæ*, *Fazia*, *Allograptella*, *Claraplumula*, *Rhodendorfia*, *Therantha*, *Allobaccha*.

### A key to the groups of the Syrphinae.

1. Face bituberculate, the front greatly produced, the scutellum vesiculous and the abdomen inflated ..... *Cyphipeltæ* Bigot. 2
- Face with a single tubercle or none ..... 2
2. Abdomen emarginate at least upon the fourth and fifth segments, caused by a sublateral crease on either side. In cylindrical or petiolate species the crease may be restricted to the terminal segments ..... 3
- Abdomen non-emarginate, the segments rolled downward laterally. 4
3. Metasternum pilose, the hairs sometimes scant ..... 5
- Metasternum bare or pubescent ..... 8
4. Metasternum pilose, the hairs sometimes scant ..... 23
- Metasternum bare or pubescent ..... 30
5. Antennæ elongate, the third segment about three times as long as wide; face produced forward, obliquely from above, upon the lower two-thirds. Front of females much more narrow than face. Abdomen convex and cylindrical and micropunctate. Very small, somewhat punctate flies with only a trace of emargination upon the broader species ..... *Paragus* Fabricius.
- Not with elongate antennæ and also produced face and punctate surface ..... 6
6. Face produced forward and diagonally upward from the epistoma, the face bluntly conical. Abdomen quite flattened and widely oval ..... *Asarcina* Macquart.
- Face not produced forward. Abdomen usually a little convex.... 7
7. Hypopygium much enlarged and asymmetrical to the right ..... *Eupeodes* Osten-Sacken.
- Hypopygium not enlarged ..... *Metasyrphus* Matsumura. 9
8. Eyes thickly long pilose; abdomen never spatulate ..... 9
- Eyes usually bare or sometimes with short pile; abdomen oval, spatulate or petiolate ..... 10
9. Face considerably produced upon the lower half, the upper face concave, sloping gently forward, the tubercle laterally compressed. Abdomen oval. Wings with a large quadrate spot ..... *Leucozona* Schiner.
- Face short, bulbous-tuberculate below; sides of abdomen more nearly parallel. Wings immaculate ..... *Ischyrosyrphus* Bigot.
10. Abdomen oval; sides of mesonotum never sharply marked with bright, opaque yellow..... 11
- Abdomen cylindrical, slender, spatulate or petiolate ..... 17
11. Lower lobe of squamæ hairy above ..... *Syrphus* Fabricius.
- Lower lobe of squamæ pubescent above ..... 12
12. The abdomen very much wider than the thorax ..... *Eriozona* Schiner.
- The abdomen is scarcely or not at all wider than the thorax..... 13



- |   |                                 |
|---|---------------------------------|
| 13. The abdomen is very convex .....  | <i>Dideoides</i> Brunetti.      |
| The abdomen is comparatively or quite flattened .....   | 14                              |
| 14. The lower face is more produced, the tubercle large; third vein strongly looped or dipped; costa and third vein end at top of wing .....  | <i>Asiodidea</i> Stackelberg.   |
| Lower face not produced; tubercle of moderate size .....  | 15                              |
| 15. Wings glassy, the villi absent or nearly so; head and particularly the front inflated .....   | <i>Scaeva</i> Fabricius.        |
| Wings villose; front not inflated .....   | 16                              |
| 16. Third antennal segment elongate .....   | <i>Didea</i> Macquart.          |
| Third segment of normal length .....  | <i>Metasyrphus</i> Matsumura.   |
| 17. Abdomen cylindrical, spatulate, or ovate-spatulate, and at least wider apically than basally .....  | 18                              |
| Abdomen petiolate, the base considerably constricted. Emarginate only upon the terminal segments .....  | <i>Baccha</i> Fabricius.        |
| 18. Usually large black flies; brightly marked yellow, the sides of the mesonotum sharply, brightly and contrastingly marked with yellow .....  | 19                              |
| Not so characterized; comparatively small flies .....   | 21                              |
| 19. Abdomen large, cylindrical; wasp-like flies .....   | <i>Doros</i> Meigen.            |
| Flattened spatulate species .....   | 20                              |
| 20. Eyes short pilose .....   | <i>Olbiosyrphus</i> Mik.        |
| Eyes bare .....   | <i>Xanthogramma</i> Mik.        |
| 21. Abdomen with nearly parallel sides, or narrowly oval; costa and third vein ending above the wing apex; hind trochanter of male with a long spur. Mesonotal margins bright opaque yellow.....  | <i>Ischiodon</i> Sack.          |
| Abdomen oval or petiolate; or if parallel-sided the third vein ends at wing apex .....  | 22                              |
| 22. Face produced forward on lower half or two-thirds; face peaked or conical, the tubercle often laterally compressed .....  | <i>Mesogramma</i> Loew.         |
| Face not produced forward; face short and tuberculate, or non-tuberculate and rounded and retreating in profile .....   | <i>Baccha</i> Fabricius.        |
| 23. Antennae elongate, the third segment about five times as long as wide; hind tibia pennate with a copious fringe .....   | <i>Afrosyrphus</i> Curran.      |
| Antennae not so lengthened; hind tibia not pennate.....   | 24                              |
| 24. Antennae elongate and the third segment about three times as long as the first. Face produced forward obliquely from above upon the lower two-thirds; front of female much narrower than face. Abdomen convex and cylindrical or broad, and micropunctate. The broader species have a trace of emargination ..... | <i>Paragus</i> Fabricius.       |
| Not with elongate antennae and also convex, micropunctate abdomen.  | 25                              |
| 25. Epistoma and the subtuberculate portion of face produced forward and usually diagonally upward; oral opening narrow and elongate .....  | 27                              |
| The face is short, the tubercle low, the oral tip of epistoma less prominent forward than the tubercle .....  | 26                              |
| 26. Sides of mesonotum dark in ground colour, the notopleura sometimes golden pollinose or micropubescent, fourth abdominal segment usually with oblique spots and paired medial vittae.....  | <i>Allograpta</i> Osten-Sacken. |
| Sides of mesonotum yellow in ground colour; fourth segment not so marked .....  | <i>Epistrophe</i> Walker.       |

27. Hypopygium of male greatly enlarged and usually oval-bulbous.  
Quite small flies, the males cylindrical. Whole lower two-thirds  
of face produced and blunt; epistoma but little or not at all  
diagonally elevated ..... [and Serville.  
*Sphaerophoria* St. Fargeau  
Hypopygium not produced ..... 28
28. Large, rather oval flies; antennae widely separated at origin ..... 29  
Small, slender species, the sides nearly parallel; antennae variable. *Metepistrophe* subg. n.  
*Claraplumula* Shannon.  
29. Cheeks large, expansive, front inflated..... *Fazia* Shannon.  
Cheeks not large; front normal ..... 30
30. Antennae elongate, the surface of abdomen and thorax micro-  
granulate; minute cylindro-convex flies ..... *Paragus* Fabricius.  
Antennae not elongate, with the surface of the abdomen micro-  
punctate ..... 31
31. Epistoma produced forward..... 32  
Epistoma not produced forward, but the face sometimes peaked .. 35
32. Epistoma produced into a sharp, slender, porrect snout..... *Rhinobaccha* de Meijere.  
Lower face produced forward, and sometimes diagonally upward.. 33
33. Abdomen petiolate ..... *Rhinoprosopa* Hull.  
Abdomen slender, with parallel sides. Small flies ..... 34
34. Eyes holoptic; notopleura bullose ..... *Carposcalis* Enderlein.  
Eyes dichoptic; notopleura without distinct bulla ..... *Tuberculanostoma* Fluke.
35. Abdomen petiolate, and constricted or narrowed basally, or at least  
narrowly spatulate, the abdomen gradually and slightly widening. 42  
Abdomen oval, or with approximately parallel sides..... 36
36. Eyes pilose (including *Ischyroshyphus* Bigot) ..... *Epistrophe* Walker.  
Eyes bare ..... 37
37. Abdomen usually nearly cylindrical; species with predominant  
fascia or paired spots of brown or yellow. Anterior four femora,  
tibiae and tarsi always simple. Face almost always yellow, the  
sides of the mesonotum yellowish ..... *Epistrophe* Walker.  
Abdomen with parallel sides or oval. Black, brown, or metallic-  
black species. Face and thorax without lighter colour..... 38
38. Lower two-thirds of face produced forward and peaked, occasionally  
reaching beyond the antennae (including *Toxomerus*) ..... *Mesogramma* Loew.  
Face short ..... 39
39. Face retreating, the abdomen oval ..... *Xanthandrus* Verrall.  
Face bulbo-tuberculate below, the abdomen oval or with parallel sides. 40
40. Face with transverse grooves or creases; antennae elongate,  
especially upon the first and third segments ..... *Rhysops* Williston.  
Face without such grooves; antennae short ..... 41
41. Anterior tibiae of males dilated, or their basitarsi enlarged and  
expanded ..... [and Serville.  
Anterior tibiae and tarsi simple and normal..... *Platycheirus* St. Fargeau  
*Melanostoma* Schiner.
42. Third vein with a shallow dip; apical cross-vein sinuous; terminal  
segments of abdomen convex; front moderately produced..... *Mimocalla* Hull.  
Third vein with usually a deep kink, the apical cross-vein sharply  
sigmoid, the apical abdominal segments more flattened, the front  
much produced ..... *Salpinogogaster* Schiner.  
Third vein almost never dipped or kinked; in any case the  
hypopygium is not enlarged ..... 43
43. Apical cross-vein and marginal cross-veins recessive, confluent some  
distance from the margin of wing, the former usually rectangular. *Calostigma* Shannon.  
These cross-veins not recessive ..... 44



44. Hind tibiae of male fractate, the fracture with a setate protuberance,  
hind tibiae of female constricted subapically ..... *Spathiogaster* Rondani.  
Hind tibiae normal ..... 45
45. Second antennal segment elongate, about as long as third segment. *Therantha* Hull.  
Second antennal segment short ..... 46
46. Abdomen of female with the last five segments greatly elongated.. *Pelecinobaccha* Shannon.  
Abdomen of female normal ..... *Baccha* Fabricius.

### Tribe SYRPHINI.

#### SYRPHUS Fabricius.

*Syrphus* Fabricius, *Systema Entomologica*, 762, 172 (1775).

*Head* : face gently bulging below, with a low tubercle ; face usually yellow ; frequently micropubescent. *Antennae* short, the third segment oval. *Thorax* : humeri and area between without pile ; pollinose medial vittae often present. Scutellum largely convex and semicircular. Lower lobe of squamae with pile amid the pubescence. *Abdomen* : oval, rather flattened. *Legs* : hind femora slender, unarmed ; hind tibiae and tarsi simple. *Wings* : hyaline, without pattern ; third vein barely sinuous.

Medium-sized species of 8 to 15 mm. which are almost always brightly marked with yellow, especially in the form of bands, broken or interrupted, or of paired spots upon the abdomen. These flies approach closely the concept for the generalized type of Syrphid. Several fossil species have been described. Abdomen as today limited, usually oval. Genotype—*Musca ribesii* Linnaeus.

Distribution : many described species from all the life realms : palaearctic 113 ; nearctic 19 ; neotropical 54 ; Ethiopian 21 ; oriental 67 ; Australian 19 ; Oceania 5 ; holarctic 6 ; fossil species 14. Many of the species listed for the regions other than nearctic (which have been mostly checked) will undoubtedly find their way into *Epistrophe* or some other group. Consequently the figures for the other regions contain the large residue of species now in *Syrphus* which have never been critically analyzed. The nearest figure contains a few older species of uncertain distinction.

Not recognized : the species upon which the following groups were based may properly belong under *Metasyrphus* instead of *Syrphus* ; insufficient data was given.

*Eusyrphus* Matsumura, *Ent. Mag. Japan* (Kyoto), 3, 20 (for *cingulatus* Mats.).

This form was based upon the wide head, much wider than the thorax, and the wide face, pilose eyes, vertex elevated, the ocelli in an equilateral triangle, third antennal segment round, equal to the first and second segments together.

*Macrosyrphus* Matsumura, *Ent. Mag. Japan* (Kyoto), 3, 23 (for *okinawae* Mats.).

This form was based upon flies with eyes bare or pilose, the male upper ommatidia subequal to the lower ones, the vertex of male very narrow, as long as the holoptic length, the anterior ocellus smaller and remote from the other two.

*Parasyrphus* Matsumura, *Ent. Mag. Japan* (Kyoto), 3, 39 (for *aeneostoma* Mats.).

This form was based upon pilose eyes, upper facets subequal to lower ones, vertex in an equilateral triangle, ocelli in an equilateral triangle, the third vein ending exactly at apex.

*Conosyrphus* Matsumura (for *okunii* Mats.).

Based upon wholly insignificant differences of proportions of the front and length of antennae ; eyes pilose.

*Syrphidis* Goffe, *Trans. Ent. Soc. S. Engl.* **8**, 78 (1933).

I cannot see the slightest reasons for changing such long and established names as *Syrphus*, *Eristalis*, *Xylota*, etc. This is particularly meaningless where the change involved (after long current use) is a change to some name created by the same author. The amount of energy involved in digging up century-old name-changes could be spent better. There should be a time-limit on such changes.

Not seen : *Dasysyrphus* Enderlein (subgenus), *S.B. Ges. Naturf. Fr. Berlin*, 208 (1937), for *ussuriensis* Enderlein. The author has not seen a description of *Dasysyrphus* which was given as a subgenus of *Syrphus*.

#### Genus METASYRPHUS Matsumura.

*Metasyrphus* Matsumura, *Ent. Mag. Japan* (Kyoto), **2**, 147 (1917).

In size, type of coloration and general appearance similar to *Syrphus* Fabricius. Distinguished principally by the bare or pubescent metasternum and the emarginate or creased sides of the abdomen, the sides not rolled over ; squamae bare. It is possible that *Metasyrphus* should be regarded as a subgenus of *Syrphus*. Genotype—*Syrphus corollae* Fabr.

Distribution : palaearctic 18 ; nearctic 48 ; holarctic 4 ; probably many other palaearctic species from *Syrphus* belong here.

Recognized subgroups : *Scaeva* Fabricius (subgenus), *Syst. Antliat.* **248**, 57 (1805).

This is a small group of flies like *Metasyrphus*, larger in size than usual, with greatly inflated front and glossy wings which are practically or entirely without villi. Eyes pilose. Subgenotype—*Musca pyrastris* Linnaeus.

Distribution : palaearctic 6 ; nearctic 2 ; neotropical 4 ; oriental 1 ; holarctic 1.

*Eristalosyrphus* Matsumura (subgenus), *J. Coll. Agric. Sappora*, **3**, 15 (1918).

Said by Matsumura to resemble *Scaeva*. Face broad, ocelli widely separated. Third antennal segment longer than the first two. Eyes bare. These differences are trivial and unimportant, but the abdomen was said to be much arched and convex (vaulted), about as wide as thorax. This is in great contrast to the markedly flattened abdomen of *Scaeva*. Villi of wings not mentioned. Subgenotype—*griseofasciatus* Mats.

*Eupeodes* Osten-Sacken (subgenus), *Bull. U.S. Geol. Surv.* **3**, 328 (1877).

These are small *Syrphus*-like flies with yellow face, and abbreviated, blackish middle stripe. Their sole distinction rests upon the greatly enlarged, polished male hypopygium, the apex of the fifth segment being subcylindrical, and the terminal part of the abdomen slightly asymmetrical. Genitalia distinctive with very long styles. The abdomen is oval and quite emarginate but the metasternum is quite hairy. Subgenotype—*volucris* O.-S.

Distribution : nearctic and neotropical 1.



*Leucozona* Schiner (subgenus), *Wien Ent. Mschr.* **4**, 214 (1860).

These are wide, spatulate flies, the abdomen quite emarginate, and the metasternum bare. They have a characteristic appearance, the base of the abdomen pellucid, the abdomen in part opalescent. The face is as much produced downward as forward, and being without definite tubercle, the face is rather concave, and is somewhat compressed just above the epistoma. Antennae short; venation rather *Syrphus*-like. Subgenotype—*Musca lucorum* Linnaeus.

Distribution: palaearctic 1; nearctic 1; holarctic none; fossil species 1.

*Ischyrosyrphus* Bigot (subgenus), *Ann. Ent. Soc. Fr.* (6), **2** (1882).

*Karosyrphus* Matsumura, *J. Coll. Agric. Sapporo*, **8**, 1, p. 9, Taf. 1, 2 (1918) (for *miyakei* Mats.).

These are rather large *Syrphus*-like flies, with distinctly emarginate abdomen in the genotype, bare or pubescent metasternum, and submetallic, submelanic coloration, especially upon the abdomen which gives them a distinct facies. Eyes pilose. Head and venation *Syrphus*-like. Face yellow; thorax, except scutellum, dark and submetallic. This is a weakly characterized group; the two American, more slender species, have the abdomen distinctly more emarginate. The author regards this as an indication of the essential weakness of this character. It would be ridiculous to separate these species on this basis; it is even questionable whether *Ischyrosyrphus* should be recognized at all. Subgenotype—*Musca glaucius* Linnaeus.

Distribution: palaearctic 6; nearctic 2; oriental 1.

*Betasyrphus* Matsumura (subgenus), *Ent. Mag. Japan* (Kyoto), **2**, 143 (1917) (for *serarius* Wied.).

*Dasyepistrophe* Szilady, *Ann. Mus. Nat. Hung. (Zool.)*, **33**, 59 (1940).

This form was based upon the pilose eyes, the elongate third antennal segment, longer than the first and second together, male vertex elevated, third vein straight, ending near the apex, besides other very minor specific variations.

Not recognized: *Posthosyrphus* Enderlein, *S.B. Ges. naturf. Fr. Berl.* **1937**, 204 (for *Metasyrphus americanus* Wied.).

#### MESOGRAMMA Loew.

*Mesogramma* Loew, *Berl. Ent. Z.* **60**, 157 (1865).

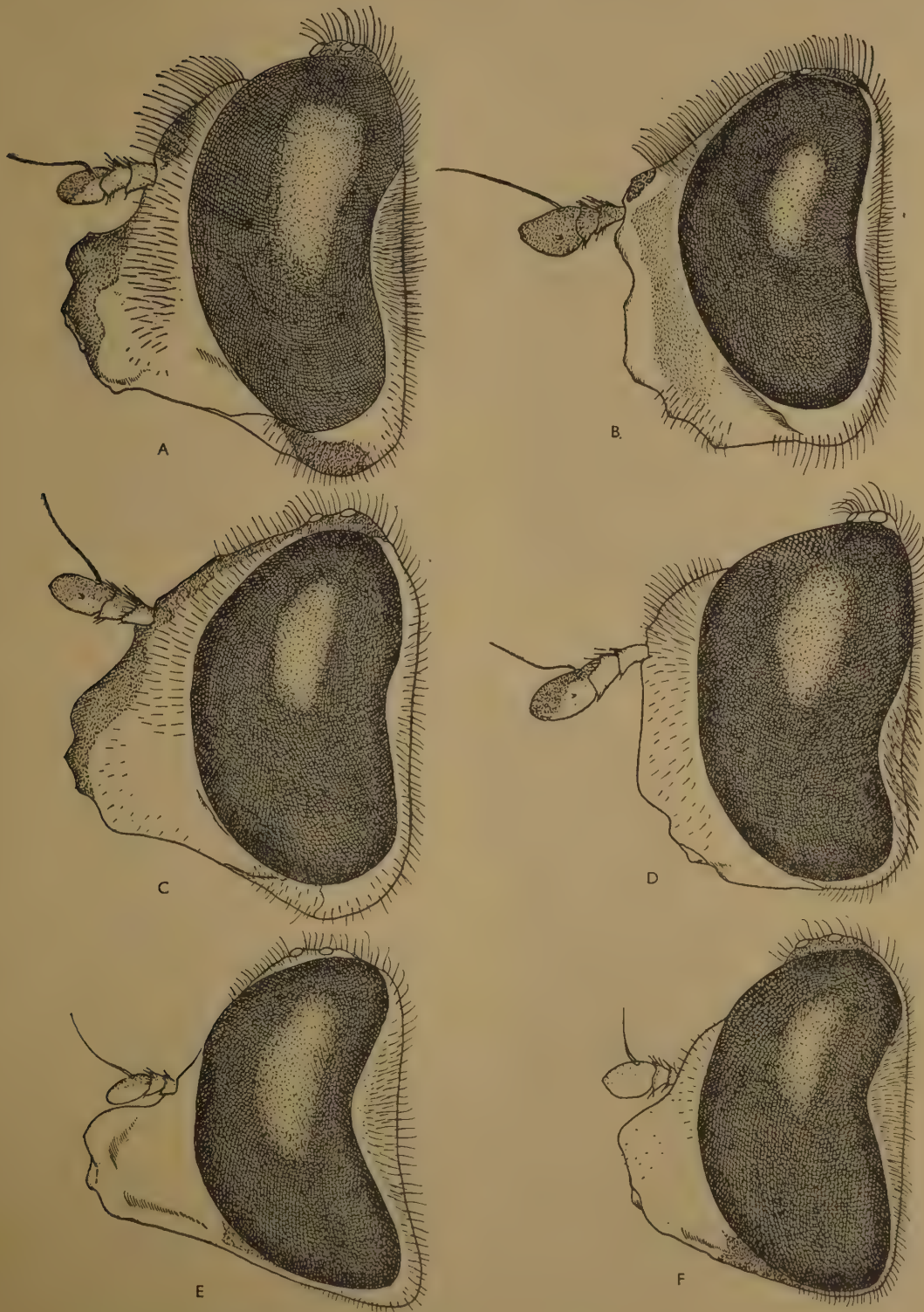
Small flies (usually under 8 mm.) with yellow face, rarely darker centrally, the face produced bluntly or acutely. Abdomen usually yellow or orange, marked with black or brown spots or fascia or vittae or a combination. Numerous patternal types exist, and species variations concern both effacement of pattern as well as to some extent variation in pattern. Abdomen oval, to subcircular, but more often slender, or even subpetiolate or spatulate. Legs simple (except *Toxomerus*). Wings with third vein usually gently sinuous. Genotype—*Syrphus boscii* Macquart.

Distribution: nearctic 5; neotropical 119; introduced into Oceania in a few cases. Two species described from New Caledonia belong elsewhere.

Recognized subgenera: *Toxomerus* Macquart, *Dipt. Exot. Supp.* **5**, 92 (1855).

*Mesogramma*-like flies, in which the males have thickened, arcuate hind femur with

Fig. 8.



## The Subfamily Syrphinae.

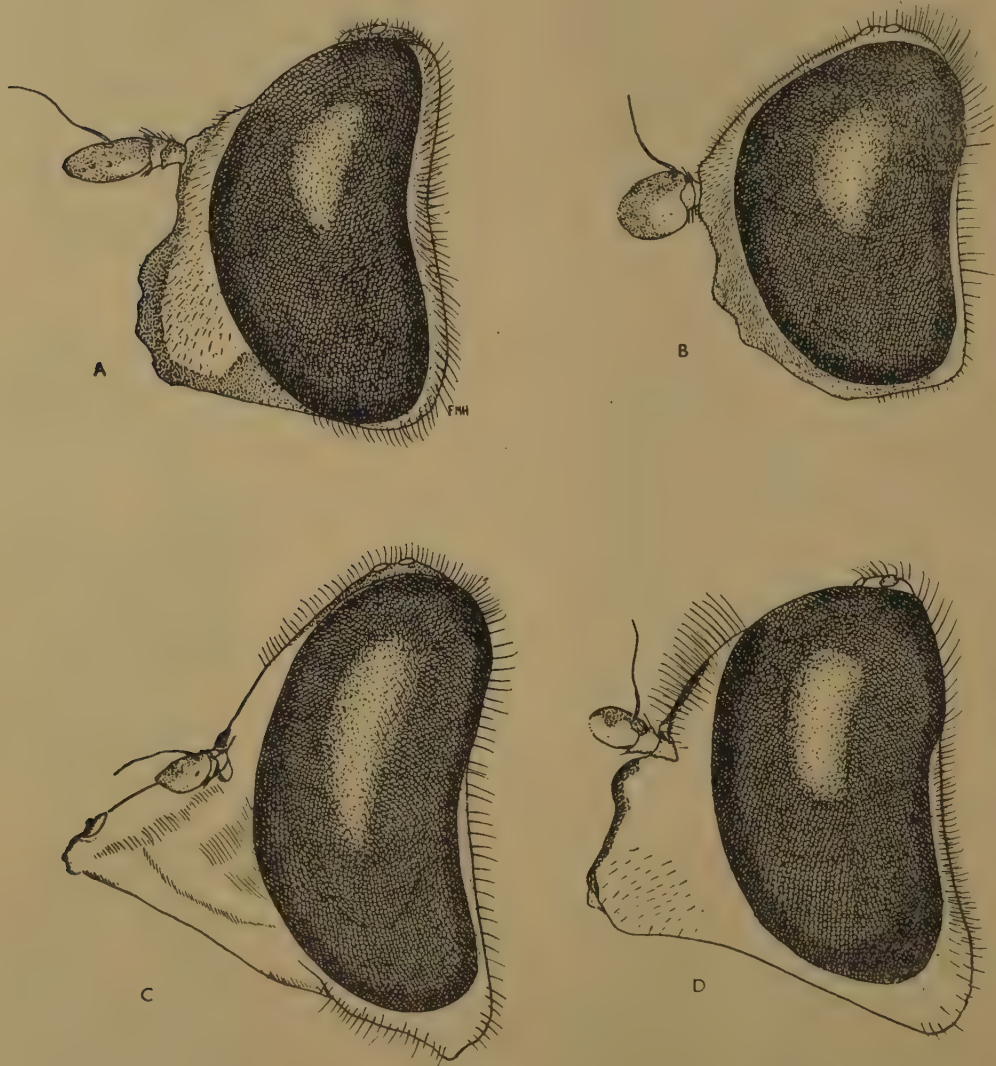
- A. *Metepistrophe remigis* Fluke, profile of head (paratype) ; B. *Epistrophe grossulariae* Meigen, profile of head ; C. *Metallograpta colombia* Curran, profile of head ; D. *Allograpta obliqua* Say, profile of head ; E. *Mesogramma* sp., profile of head ; F. *Mesogramma marginata* Say, profile of head.



an elongated basal protuberance more or less paralleling the femur, and with arcuate hind tibiae, the apex flared and scoop-like. Abdomen either narrow or wide oval. Venation *Mesogramma*-like. Subgenotype—*Mesogramma geminata* Say.

Distribution : nearctic 3 ; neotropical for one species.

Fig. 9.



The Subfamily Syrphinae.

- A. *Dioprosopa clavata* Fabricius, profile of head ; B. *Baccha elongata* Fabricius, profile of head ; C. *Rhinoprosopa flavophylla* Hull, profile of head (holotype) ; D. *Rhinoprosopa aenea* Hull, profile of head (paratype).

*Hybobathus* Enderlein (subgenus), *S.B. Ges. naturf. Fr. Berl.* 1937, 233.

Based upon the swollen, bulging protuberance of the anterior front, separated from the posterior part by a crease. While hardly a character of much weight it

Fig. 10.



## The Subfamily Syrphinae.

- A. *Asarcina rostrata* Wiedemann, profile of head ; B. *Asarcina* sp., profile of head ; C. *Carposcalis ecuadoriensis* Fluke, profile of head (paratype) ; D. *Melanostoma pictipes* Bigot, profile of head ; E. *Leucopodella lanei* Curran, profile of head ; F. *Sphaerophoria cylindrica* Say, profile of head.



is here recognized as a subdivision of *Mesogramma*. Subgenotype—*quadrilineatus* Enderlein.

Not recognized : *Antips* Enderlein, *S.B. Ges. naturf. Fr. Berl.* **1937**, 228 (for *Mesogramma sapphiridiceps* Bigot).

Based upon slender male front, the microholoptic males, the curved third vein, and the somewhat swollen antennal base, etc. The several characters given are not here valued at more than a species group.

Not recognized : *Mitrosphen* Enderlein, *S.B. naturf. Fr. Berl.* **1937**, 227 (based on *Mesogramma tibicen* Wied.).

Based on the slender front, convex front, macroholopticism, the convex third vein, etc. These characters are held by the author to deserve a species group valuation. The author mentioned three species with this ensemble but that fact in itself does not make the characters worth more.

#### XANTHOGRAMMA Mik.

*Xanthogramma* Mik, *Wien Ent. Mschr.* **4**, 215 (1860).

Medium-sized *Syrphus*-like flies, brightly marked with opaque, canary yellow on thorax and abdomen contrasted with black ; metasternum bare. Face and legs predominantly yellow. Third antennal segment short with about as much area as the first two segments or less ; arista short. Abdomen wide spatulate and strongly emarginate. Wing venation similar to *Syrphus*. Lateral margin of thorax bright yellow, the upper post-margin of mesopleura ridged. Subgenotype—*Syrphus ornatus* Meigen.

Distribution : palaearctic 10 ; nearctic 1 ; Ethiopian 12 ; oriental 7 ; Australasian : (Oceanic) 2. Some of these species probably should not remain in *Xanthogramma*.

*Olbiosyrphus* Mik (subgenus), *Wien Ent. Ztg.* **16**, 66 (1897).

A *Xanthogramma* with hairy eyes. This is the sole characteristic upon which this name rests. It is therefore upon a very weak basis. Still, if we admit the use of ocular pile as a basis for divisional status in other subfamilies (*Cheilosinae*, etc.), we must do so here. Subgenotype—*Syrphus laetus* Fabricius.

Distribution : palaearctic (2), one from Europe, one species French Indo-China.

The flies of the genus *Xanthogramma* would be largely separated from *Syrphus* only upon a distinctive type of coloration, except that the abdomen of the genotype and related European species and one nearctic species are really spatulate. In the genotype and one or two other species the post-callar crease is exceptionally deep, leaving the ridge especially prominent. Undoubtedly, many of the species that have been placed here must go into other existing groups. *X. fasciatum* Shiraki has the metasternum pilose.

*Ischiodon* Sack (subgenus), *Ent. Mitt.* **2**, 5 (1913).

This name was proposed for a small species of *Xanthogramma*-like fly upon the basis of the males bearing a slender spur upon the hind trochanters. This is a wholly untenable character. However, it may be noted that the costa ends a considerable distance before the apex of the wing, as much perhaps as in *Microdon*,

or *Volucella*. This appears to be the only character upon which the name might be retained. Subgenotype—*Scaeva scutellare* Fabricius.

Distribution: Ethiopian, oriental, Australian. One species, the status of two other names undecided.

*Simosyrphus* Bigot (subgenus), *Ann. Soc. Ent. Fr.* (6), 2, *Bull.* LXVIII, 4 (1882).

This subgenus was separated from *Syrphus* on the non-tuberculate face and the third antennal segment which is two or more times as long as wide. Subgenotype—*grandicornis* Macquart. Oceania and Australia.

#### DOROS Meigen.

*Doros* Meigen, *Illigens Mag. f. Insektenkunde*, 2, 274–76 (1803).

Large, wasp-like flies, black with bright yellow markings. The face is *Syrphus*-like and the antennae are short, the third segment about as long as wide. Eyes bare. The thorax has bright yellow lateral margins. Metasternum bare. Abdomen elongate, subcylindrical, more emarginate except upon the fifth segment. Abdomen brightly marked with yellow fascia. Legs and wing venation *Syrphus*-like. Genotype—*Syrphus conopseus* Fabricius.

Distribution: palaearctic 1; nearctic 1; neotropical 1 (probably incorrect); oriental 1.

#### DIDEA Macquart.

*Didea* Macquart, *Suite Buffon*, 1, 508–15 (1854).

Medium-sized flies with face chiefly yellow and often with a black stripe. Face tuberculate, the eyes usually bare (bare in genotype), the third antennal segment longer than the first two segments. Metasternum bare. Abdomen widely oval but rather flattened and strongly emarginate. The pattern of most species follows a rather characteristic type. Wing venation *Syrphus*-like except that the third vein is strongly sinuous and in some species looped. Genotype—*fasciata* Macquart.

Distribution: palaearctic 5; nearctic 5; neotropical 1; oriental 1; holarctic 2; *Didea* is possibly not more than a subgenus of *Metasyrphus*.

Recognized subgenera: *Dideoides* Brunetti, *Rec. Indian Mus.* 2, 54 (1908).

This group contains oriental species of *Didea*-like flies in which the abdomen is markedly convex and yet strongly emarginate. The convexity of the abdomen suggests *Chrysotoxum*. The third vein is dipped, but so it is in several *Didea* (notably *coquilletti*) and also in *Metasyrphus annulipes*. *Dideoides* may be regarded as a highly modified *Didea*, or as a separate development from *Syrphus*-like types, but hardly as a transition between the two. Subgenotype—*ovata* Brunetti.

Distribution: oriental 8.

*Asiodidea* Stackelberg, *Konowia*, 9, 224 (1930). Illustrated.

These are *Didea*-like flies in which the lower face is rather strongly produced, leaving the oral opening elongate. The tubercle of the face is larger, the face below the antennae weakly hollowed out. Eyes bare. The mesonotum has broad, yellow sides, the humeri bare. The abdomen is oval and emarginate. The third



vein is strongly looped or dipped. The costa and third vein end beyond the tip of the wing, the subapical cross-vein is strongly curved. Subgenotype—*patanini* Stackelberg.

Distribution: palaearctic (China) 1.

Not recognized: *Malayomyia* Curran, *J. F.M.S. Mus.* **14**, 225 (1928).

This appears to be a *Dideoides* differing in minor details of the face and the mere fact that the abdomen is without pattern. The wings have only a trace of a curve downward. The abdomen is of the same broad, short, oval, convex, emarginate type. The face has two very prominent slits at the lower end of the stripes close to the cheeks. Based on *pretiosa* Curran.

#### ERIOZONA Schiner.

*Eriozona* Schiner, *Wien Ent Mschr.* **4**, 214 (1860).

Large flies of dark coloration except the yellow face (in the known species) and with exceptionally wide, short, strongly emarginate abdomen which is rather flattened. The abdomen is considerably wider than the thorax. Head about as wide as thorax, the face *Syrphus*-like with low tubercle. The third segment of the antennae is a little longer than the final two segments combined. Eyes bare. The wing venation is *Syrphus*-like with the third vein a little sinuous. Genotype—*Scaeva syrphoides* Fallen.

Distribution: palaearctic 1; oriental 4.

#### ASARCINA Macquart.

*Asarcina* Macquart, *Dipt. Exot.* **2**, Pt. 2, 77 (1842).

Rather large flies, very largely light coloured with exceptionally flat, oval abdomen. The head has the face produced in a peak upon the lower half and weakly tuberculate. Third antennal segment weakly tuberculate. Eyes usually bare. Metasternum pilose. Abdomen oval, much flattened, the sides emarginate, though weakly. Hypopygium small. Legs simple. Wings with venation much like *Syrphus*. Genotype—*Scaeva rostrata* Wiedemann.

Distribution: palaearctic 3; Ethiopian 14; oriental 10; Australian 1 or more; Oceania 2; fossil species 1.

*Dideopsis* Matsumura (subgenus), *Ent. Mag. Japan*, **4**, 142 (1917).

An *Asarcina*-like fly with short, undeveloped face like *Syrphus*. Subgenotype—*Eristalis aegrotus* Fabr. Two species (one undescribed), both Indomalayan.

Not recognized: *Achaonus* Munro, *Ann. Transv. Mus.* **10**, 87 (1924), based upon the presence of a collar of hairs across the mesonotum just behind the humeri and the less curved third vein, longer vertical triangle, etc. This collar is paralleled in *Baccha*. Based on *hulleyi* Munro.

#### Genus EPISTROPHE Walker.

*Epistrophe* Walker, *Insecta Saundersiana Dipt.* **1**, 242 (1852).

Slender, mostly small-sized species, with the bright markings characteristic of *Syrphus* and with the lateral margins of the abdomen down-rolled, accentuating their slender appearance. Metasternum hairy; otherwise structurally similar to *Syrphus*. Genotype—*Syrphus grossulariae* Meigen.

Distribution : palaearctic 16 ; nearctic 43 ; neotropical 21 ; Ethiopian 1 ; holarctic 8. An indeterminate number of species believed to occur in the unanalyzed residue of the genus *Syrphus*.

Recognized subgroups :

*Allograpta* Osten Sacken (subgenus), *Bull. Buffalo Soc. Nat. Hist.* 3, 49 (1876).

Large as the assemblage of *Allograpta* species are, I cannot see any valid distinctions in the genotype except upon the abdominal pattern for this group. There are numerous species of *Allograpta* as well as of *Epistrophe* in which the epistoma is thrust forward peak-like. Such species of *Epistrophe*-like flies and non-*Allograpta*-like pattern have been called *Fazia* (*Fazia* Shannon) where the abdomen is oval. *Fazia* becomes then a subgenus of *Epistrophe*. If it is desirable to segregate the forms with slender, narrow abdomen and jutting epistoma, it may be done under the name here proposed as *Metepistrophe*. If we recognized *Allograpta*, what will we do logically with the numerous well-defined patterned types of *Baccha* which have clearly had a long and associated history? Perhaps *Allograpta* should be regarded as a species group within *Epistrophe*. Subgenotype—*Scaeva obliqua* Say.

Distribution : nearctic 3 ; neotropical 32.

*Fazia* Shannon (subgenus), *Proc. U.S. Nat. Mus.* 70, No. 9, p. 25 (1927).

Oval, wide, species of *Epistrophe*-like flies in which the markings are bright and the epistoma is produced strongly forward. Subgenotype—*bullaeophora* Shannon.

Distribution : neotropical 9.

*Metallograpta*, new subgenus. This name is proposed for the species of *Allograpta* in which the epistoma juts forward. Subgenotype—*Allograpta colombia* Curran.

*Metepistrophe*, new subgenus. This name is proposed for the species of *Epistrophe* in which the epistoma juts forward. Subgenotype—*Epistrophe remigis* Fluke.

*Chasmia* Enderlein (subgenus), *S.B. Ges. naturf. Fr. Berl.* 1937, 213.

These appear to be *Allograpta*-like flies in which the epistoma is produced forward, diagonally, the oval opening hence several times as long as wide. It is related, though perhaps not directly, to *Metepistrophe*, in which the same condition is found with an oval abdomen. (Subgenotype—*hians* Enderlein). The reduction of the plumula, the squamal pile mentioned by Enderlein, I consider of no importance.

*Claraplumula* Shannon (subgenus), *Proc. U.S. Nat. Mus.* 70, No. 9, p. 8 (1927).

These are oval, large, *Epistrophe*-like flies with the front inflated, the cheeks usually large but both face and front considerably produced forward. The antennae arise a little farther apart than usual. Subgenotype—*latifacies* Shannon.

Distribution : neotropical 1.

*Allograptina* Enderlein (subgenus), *S.B. Ges. naturf. Fr. Berl.* 1937, 204.

Third antennal segment elongate, nearly three times as long as wide. Erected as a genus for *octomaculata* Enderlein from Mexico.



*Phalacrodira* Enderlein (based on *Epistrophe tarsata* Zett.), *S.B. Ges. naturf. Fr. Berl.* **1937**, 205.

Based upon the pilose eyes, male genitalia being a little larger, the penis a little longer, pile of slightly different length upon the mesonotum, etc.

Not recognized: *Euryepistrophe* Szilady (subgenus), *Ann. Mus. Nat. Hung.* **33**, 59 (1940).

Based only on the oval abdomen, in contrast to the usual narrow, slender form. No species was given as subgenotype but three species were mentioned in this order: *nitidicollis* Mg., *diaphana* Zett., *grossulariae* Mg. The first may be here designated the type. Erected as a subgenus by Szilady

Not recognized: *Heterepistrophe* Szilady (for *cretensis* Zett.), *Ann. Mus. Nat. Hung.* **28**, 59 (1940).

Based purely upon the paternal characteristics of the abdomen, the number of bands, etc. These are purely specific characteristics and need no supraspecific categories with a name.

Not recognized: *Episyrphus* Matsumura, *Ent. Mag. Japan* (Kyoto), **3**, 16 (1917) (for *balteatus* Deg.).

This form was based as follows: lower part of face in male not beak-like produced; vertex in the female much narrower than the half breadth of the front between the antennae; the third antennal joint somewhat longer than the first and second taken together, the arista narrower and not pubescent. Wings nearly the same as that of *Stenosyrphus*.

#### SPHAEROPHORIA St. Fargeau and Serville.

*Sphaerophoria* St. Fargeau and Serville, *Encycl. Method.* **10**, 513 (1825).

These are small, slender flies, subcylindrical in the males. Face yellow except rarely, and with bright yellow markings upon the thorax and abdomen. Head with the face peaked forward from the lower half as in *Mesogramma*. Antennae short. Eyes bare. Thorax with scutellar and lateral margin and pleura marked with yellow. Metasternum hairy, the quantity variable. Abdomen with a characteristic facies and characteristically with the male hypopygium greatly enlarged, oval or bulbous. Legs and wing venation as in *Mesogramma*. Genotype—*Musca scripta* Linnaeus.

Distribution: palaearctic 10; nearctic 19; neotropical 8; Ethiopian 2; oriental 7; Australian 3; Oceania 1; holartic 2.

The enlarged male hypopygium, the hairy metasternum, are the chief differences from *Mesogramma*; also the world-wide distribution.

#### Tribe BACCHINI.

##### BACCHA Fabricius.\*

*Baccha* Fabricius, *Syst. Antliat.* **199**, 44 (1805).

*Ocyptamus* Macquart, *Hist. Nat. Dipt.* **1**, 559 (1834).

Slender flies, usually petiolate, sometimes spatulate, from three to twenty

\* In a Revision of the New World Species of the Genus *Baccha* (*Entomologica Americana*, 1948), the author has erected the following related genera and subgenera: *Orphnabaccha* with genotype *Baccha coerulea* Williston, *Xestoprosopa* with genotype *Baccha delicatula* Hull, subgenus *Aulacibaccha* with subgenotype *Baccha titan* Hull, *Ocyptamus* Macquart is recognized as a subgenus.

millimetres. Coloration either dark or light or metallic. There is a large group with yellow-red face, another with face in part or wholly black. Metasternum bare. Face usually tuberculate, sometimes not. Males holoptic. Antennae short. Legs simple. Contains many species groups. Genotype—*Syrphus elongata* Fabricius.

Distribution: palaearctic 4; nearctic 12; neotropical 201; Ethiopian 24; oriental 52; Australian 4.

Not recognized: *Pseudodoros* Becker, *Mitt. Zool. Mus. Berl.* **2**, 92 (1903), based on *nigricollis* Becker.

Recognized subgroups:

*Calostigma* Shannon (subgenus), *Proc. U.S. Nat. Mus.* **70**, No. 9, p. 8 (1927).

A characteristic group of polished, quite small, usually vittate, petiolate *Baccha*-like flies in which both the lower cross-veins are markedly recessive, that is ending in the third and fourth veins some distance from the wing margin. These cross-veins are usually straight instead of sinuous. Mesonotum with micropubescent vittae; otherwise like *Baccha*. Subgenotype—*elnora* Shannon.

Distribution: neotropical 12.

*Mimocalla* Hull (subgenus), *Ent. Amer.* **23**, 46 (1943).

Petiolate, rather large, bright-coloured, wasp-like species in which the third vein is strongly curved but not kinked and the apical cross-vein is sinuous. The front is rather prominent, the face tuberculate. Rather similar to *Salpingogaster*, though the hypopygium is not prominent and the third vein is not deeply kinked or the cross-vein deep sigmoid. Subgenotype—*Baccha capitata* Loew.

Distribution: neotropical 7.

*Therantha* Hull (subgenus), *Ent. Amer.* **23**, 47 (1943).

Oval, medium-sized flies of bright colour and nearly typical venation. Face tuberculate, second and third segments of antennae of nearly equal length. Abdomen widely oval, a very short yet pronounced constriction at the base of the second segment. Subgenotype—*Baccha atypica* Curran.

Distribution: neotropical 2.

*Pipunculossyrphus* Hull (subgenus), *Psyche*, **44**, 29 (1937).

Small flies with bright markings but very large head and eyes, considerably wider than thorax. Abdomen with parallel sides. Wing longer than the reduced abdomen with the alula nearly or completely absent. Subgenotype—*globiceps* Hull.

Distribution: neotropical 2.

*Styxia* Hull (subgenus), *Ent. Amer.* **23**, 46 (1943).

Spatulate, *Baccha*-like flies of sombre colour with bare metasternum and tuberculate face and bulbous, inflated front and quite pilose eyes. Face unusually wide. Very possibly this fly may be more closely related to *Syrphus* and *Scaeva*. Subgenotype—*ebilis* Hull.

Distribution: neotropical 1.



*Spathiogaster* Rondani (subgenus), *Rev. Zool.* **6**, 43 (1843).

These are *Baccha*-like flies in which the males have curious, fractate hind tibiae, the loop with a setiferous, protuberant ornament. The face is tubercular, rather concave in the female above the tubercle. The facies and the abdominal coloration differ in the sexes. There is a slight curve in the female hind tibiae and the abdomen of the female is wider and more spatulate. Subgenotype—*Syrphus ambulans* Fabricius.

Distribution : palaearctic 3.

*Pelecinobaccha* Shannon (subgenus), *Proc. U.S. Nat. Mus.* **70**, No. 9, p. 10 (1927).

*Baccha*-like flies with tuberculate face in which the female abdomen is greatly lengthened into a long, cylindrical structure. Each segment of the abdomen except the first is lengthened, the sixth especially so. Face, antennae, venation and legs *Baccha*-like. Subgenotype—*peruviana* Shannon.

Distribution : neotropical 1.

*Dioprosopa*, new subgenus. This name is proposed for those species of *Baccha* in which the epistoma juts forward. Subgenotype—*Baccha clavata* Fabricius.

*Allobaccha* Curran (subgenus), *J. F.M.S. Mus.* **14**, 245, 251 (1928).

Curran erected this name as a subgenus of *Baccha* (subgenotype—*rubella* Wulp) for those species in which the humeri is wholly or a part pilose on the posterior half.

Distribution : oriental.

*Leucopodella*, new subgenus. This name is proposed for those species of *Baccha* which lack the facial tubercle. Subgenotype—*Baccha lanei* Curran.

Not recognized : *Atrichosticha* Enderlein, *S.B. Ges. naturf. Fr. Berl.* **1937**, 234 (for *Spathiogaster aurantiaca* Becker).

Based upon slight differences from the subgenus *Spathiogaster* of the genus *Baccha*. He gave as differences : abdomen more flattened, with trifling differences in shape, the third segment of antenna a little longer than broad, and the slender front, etc.

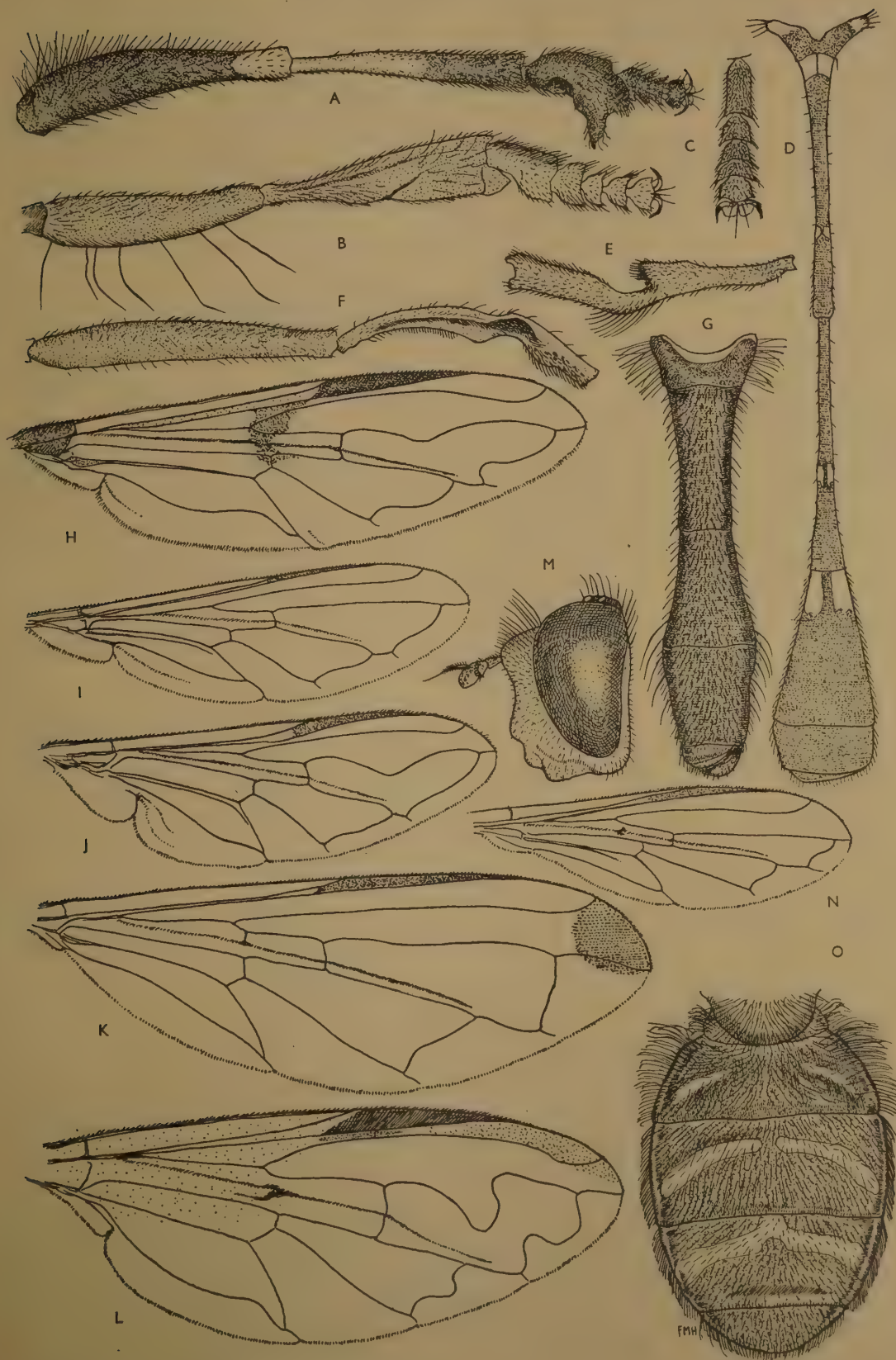
Not recognized : *Ptileuria* Enderlein, *S.B. Ges. naturf. Fr. Berl.* **1937**, 235 (for *Baccha picta* Wiedemann).

Based upon the broad wings, the narrow male front, the macroholoptic male, the shape and proportion of the abdominal segments, which are in no way unique. While the breadth of the wing is truly unusual, the various differences are not rated above species groups.

#### The Subfamily Syrphinae.

- A. *Pyrophoena granditarsis* Forster, dorsomedial view of male front leg ; B. *Platycheirus* sp., view of male front leg ; C. *Pyrophoena rosarum* Fabricius, male front tarsi ; D. *Baccha titania* Hull, abdomen (holotype) ; E. *Spathiogaster ambulans* Fabricius, male hind tibia rotated ; F. *Spathiogaster ambulans* Fabricius, male hind femora and tarsi ; G. *Spathiogaster ambulans* Fabricius, abdomen ; H. *Eosalpinogaster dactylopiamus* Blanchard, wing ; I. *Spathiogaster ambulans* Fabricius, wing ; J. *Didea fasciata* Macquart, wing ; K. *Calostigma elnora* Shannon, wing (holotype) ; L. *Salpingogaster maculipennis* Hull, wing (holotype) ; M. *Spathiogaster ambulans* Fabricius, face ; N. *Rhinobaccha gracilis* de Meijere, wing ; O. *Dideoides* sp., abdomen.

Fig. 11.





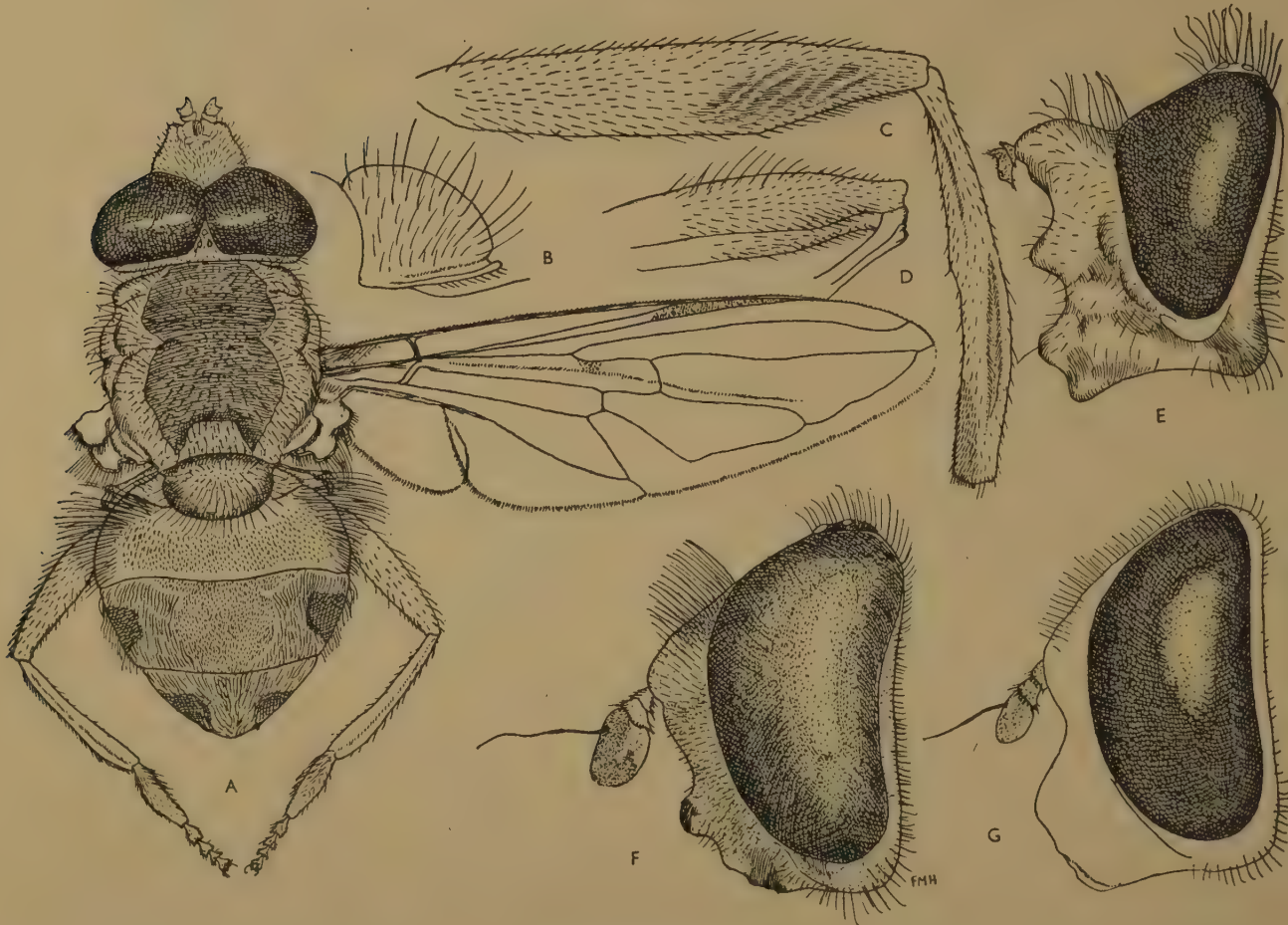
## RHINOPROSOPA Hull.

*Oligorhina* Hull, *Psyche*, **44**, 30 (1937); preoccupied in Coleoptera.

*Rhinoprosopa* Hull, *Proc. N. Eng. Zool. Cl.* **20**, 23 (1942).

Petiolate flies with yellow, peaked face, the epistoma jutting forward and upward. Face yellow, abdomen marked with yellow. Otherwise *Baccha*-like in characteristics. Metasternum bare. It will be seen that this genus resembles *Metepistrophe*

Fig. 12.



## The Subfamily Syrphinae.

A. *Cyphipelta rufocyanea* Walker, dorsal view (type); B. *Cyphipelta rufocyanea* Walker, scutellum (type); C. *Cyphipelta rufocyanea* Walker, hind femur (type); D. *Cyphipelta rufocyanea* Walker, hind femur (type); E. *Cyphipelta rufocyanea* Walker, profile of head (type); F. *Xanthandrus comptus* Harris, profile of head; G. *Asiodidea patanini* Stackelberg, profile of head (redrawn from Stackelberg).

in the face but has a bare metasternum and petiolate abdomen. It is difficult to decide whether it should be placed with *Baccha* because of the bare metasternum or with the *Epistrophe* complex and viewed as a type which has paralleled *Baccha* in the bare metasternum. Genotype—*aenea* Hull.

Distribution: neotropical 4.

## SALPINGOGASTER Schiner.

*Salpingogaster* Schiner, *Novara Reise*. Dipt. 344 (1868).

Medium-sized flies or smaller, usually bright coloured, strongly petiolate with tuberculate face and produced knob-like front. Wing venation characteristic, the third vein often deeply kinked, sometimes with a shallow loop; subapical cross-vein strongly sinuous and frequently sigmoid. Hypopygium and terminal segments of abdomen enlarged. Genotype—*pygophora* Schiner.

Distribution: neotropical 36.

*Eosalpingogaster*, new subgenus, is proposed for *S. conopida* Philippi; it includes *nepenthe* Hull, *dactylopiamus* Blanchard. Corners of first abdominal segment with a sharp hook. Third vein with only a very low curve.

## RHINOBACKHA de Meijere.

*Rhinobaccha* de Meijere, *Tijd. Ent.* 51, 315 (1908).

Small, *Baccha*-like flies with the epistoma produced forward as a porrect snout similar to but not as extreme as *Rhingia*. Genotype—*gracilis* de Meijere.

Distribution: oriental 1.

## Tribe MELANOSTOMINI.

## XANTHANDRUS Verrall.

*Xanthandrus* Verrall, *British Flies*, 8, 316 (1901).

Small to medium-sized flies, dark in colour, with often some orange markings. Face black or metallic, recessive below, microtuberculate; third antennal segment much larger than first two. Eyes bare. Notopleural and mesopleural bullae well developed. Metasternum bare. Abdomen oval, non-emarginate. Legs with hind femora tending to be slightly smaller apically. Venation *Syrphus*-like. Genotype—*Musca comptus* Harris.

Distribution: palaearctic 2; neotropical 6; Ethiopian 1; oriental 4; the nearctic region seems to be curiously skipped except as one species may probably be found in Texas.

## MELANOSTOMA Schiner.

*Melanostoma* Schiner, *Wien Ent. Mschr.* 4, 213 (1860).

Small flies with black or metallic face and usually dark coloration upon the abdomen, though sometimes with pairs of orange spots or fascia. Thorax without light markings. Head with weakly tuberculate face and the oral margin recessive. The venation is more or less like that of *Syrphus*. Genotype—*Musca mellinum* Linnaeus.

Distribution: palaearctic 32; nearctic 31; neotropical 19; Ethiopian 13; Australian 5; into Oceania 1; holarctic 3; oriental 16.



Recognized subgroups:

*Melangyna* Verrall (infragenus), *British Flies*, 8, 313 (1901).

A *Melanostoma*-like fly with two pairs of obscure yellow spots. A weakly defined subgenus at best, resting upon swollen cheeks and occiput, shorter antennae and pilose eyes. Subgenotype—*quadrimaculata* Verrall.

Distribution: palaearctic 1.

*Rhysops* Williston (subgenus), *J. N.Y. Ent. Soc.* 15, 2 (1907).

These are *Melanostoma*-like flies in which the face has one or more transverse creases below the antennae and the antennae are rather elongate, all the segments affected, though unequally. The face is recessive, weakly or not at all tuberculate, always dark, usually metallic and often with violaceous or cupreous stripes. Eyes bare, the thorax is metallic with the notopleural bullae well developed; metasternum bare. Abdomen *Melanostoma*-like often with yellow spots or fascia. Hind femora tending to slight enlargement apically. Wing venation *Melanostoma*-like, third vein rather straight, ending at apex. Subgenotype—*rugonasus* Williston. Not recognized is *Braziliana* Curran, *Ann. & Mag. Nat. Hist.* (9), 16, 252 (1925), for *M. longicorne* Will.

Distribution: neotropical 14.

*Carposcalis* Enderlein (subgenus), *S.B. Ges. naturf. Fr. Berl.* 1937, 199.

This name was given to the *Melanostoma* with produced and extended epistoma; otherwise the face is quite as in that genus. The species tend to be metallic without yellow spots upon the abdomen. Subgenotype—Enderlein gave *Stegnum* (*stegna*) Say.

Distribution: nearctic and neotropical, the number indeterminate, but with at least seven species.

*Hiratana* Matsumura (subgenus), *Ent. Mon. Mag. Japan* (Kyoto), 3, 129 (1919).

A fly which seems to differ from *Melanostoma* only in the elongate antennae and the fact that the anterior ocellus is remote from the posterior ones. Abdomen oblong, wider than thorax, quite flat. Third antennal segment twice as long as the first and second segments together. Subgenotype—4-*guttula* Mats.

*Petersina* Enderlein (subgenus), based upon *lanata* Enderlein, *S.B. Ges. naturf. Fr. Berl.* 1937, 205. A *Melanostoma*-like fly in which the eyes and body are thickly pilose; abdomen broadly oval. General appearance somewhat like *Melangyna*.

Not recognized: *Posthonia* Enderlein, *S.B. Ges. naturf. Fr. Berl.* 1937, 203, (for *longipenis* Enderlein).

Based upon the long penis and length of tergite eight of the male. The author does not believe that supra specific categories should be named upon genitalic differences. The other characters given by Enderlein, the differences between the comparative length of the wing and thoracic squamae and their pile, the relative size of the plumula, and minutiae which do not deserve group recognition.

Not recognized: *Pachysphyria* Enderlein, *S.B. Ges. naturf. Fr. Berl.* 1937, 196 (for *Melanostoma ambigua* Fallen).

Based upon the thickened hind basitarsi, the straight posterior eye border, the enlarged upper ommatidia of the male, the macroholoptic males, etc. These characters are evaluated in this study at the level of species groups and not of genera.

*Talahua* Fluke, *Amer. Mus. Novit.* 1272, 23, (1945). For *fervidum* Fluke. (Ecuador). Based upon the enlarged genitalia. Given as a subgenus of *Melanostoma*.

#### TUBERCULANOSTOMA FLUKE.

*Tuberculanostoma* Fluke, *Ann Ent. Soc. Amer.* 36, 425 (1943).

Small, submetallic, *Melanostoma*-like flies with greatly produced epistoma and in which the males are dichoptic. Notopleura without distinct bullae. These flies may possibly be regarded as peculiar types, primitive with respect to the dichoptic eyes, specialized with respect to the epistoma. Apparently they parallel *Carpocalis* to some extent. Genotype—*antennatum* Fluke.

Distribution: neotropical 2.

#### PLATYCHEIRUS St. Fargeau and Serville.

*Platycheirus* St. Fargeau and Serville, *Encycl. Method.* 10, 513 (1825).

These are slender, small or rarely medium-sized flies in which apparently the only real distinguishing character is the special modification of the male tibia and tarsi and the chaetal ornaments of the femora. It is perfectly true that the numerous species of *Platycheirus* tend to have the abdomen brightly marked with yellow, the numerous species of *Melanostoma* are frequently dark, melanic or metallic. But there are many exceptions. In *Platycheirus* the face is usually recessive, weakly tuberculate, the notopleural bullae not noticeable, the eyes bare and the metasternum bare. Subgenotype—*Syrphus scutatus* Meigen.

Distribution: palaearctic 27; nearctic 34; oriental 1; Australian 3; holarctic 7; fossil species 3.

*Pyrophaena* Schiner (subgenus), *Wien. Ent. Mschr.* 4, 213 (1860), based on *Syrphus rosarum* Fabricius.

These are essentially spatulate species of *Melanostoma*, with or without additional exaggerated male characters as in *granditarsis* Forster, and perhaps one other species. They are not greatly different from *Xanthandrus*, from which they are separated by the slight difference in the face and the shape of abdomen. Four species have been placed here; two are holarctic.

#### Remote Genera and Genera of Uncertain Relationships.

##### PARAGUS Latreille.

*Paragus* Latreille, *Hist. Nat. Crust. Insect.* 14, 359 (1804).

These are always small, dark flies, rarely with any light coloration, though the face may be pale yellow, the abdomen may be partly reddish. They are often markedly punctate especially upon the abdomen. Head with the face short, weakly produced below, scarcely tuberculate. The antennae are short, or in some species the third segment tends to become elongate. Eyes bare or pilose. Thorax dark. Metasternum pilose or bare. Abdomen usually short, the sides emarginate though curled over, leaving the abdomen bowl-shaped. The hypopygium small. In at



least one species the abdomen is longer and subpetiolate. Wing venation *Mesogramma*-like. Genotype—*Syrphus bicolor* Fabricius.

Distribution : palaearctic 18 ; nearctic 5 (two unrecognized) ; neotropical 4 (may belong elsewhere) ; Ethiopian 4 ; oriental 12 ; Australian 3 ; holartic 1.

#### AFROSYPHUS Curran.

*Afrosyrphus* Curran, *Bull. Amer. Mus. Nat. Hist.* **57**, 50 (1927).

These are medium-sized insects with tuberculate face, the front a little produced forward and the antennae quite elongate, more so perhaps than in any other member of the subfamily excepting *Rhysops*. The third segment is five times as long as wide. First and second segments also elongate, the first more so. Abdomen twice as long as wide with nearly parallel sides and non-emarginate, the sides of the segment strongly curled over. Upon the legs the hind femora are short and slightly thickened. The distal half of the hind femora and whole length of the hind tibiae above and below are equipped with a flat, grossly developed pennate brush of hairs not greatly unlike that upon *Trichopoda* in the Tachinidae. Wings with *Syrphus*-like venation. Genotype—*varipes* Curran.

Distribution : ethiopian 1.

#### ARGENTINOMYIA Arribalzaga.

*Argentinomyia* Arribalzaga, *Ann. Soc. Cien. Argent.* **32**, 40 (1893).

Quite small, rather slender, brassy-black flies with bluish black face and front. Length 7 mm. Both the first and second segments of the antennae are elongated, the second and third about equal or a little longer than the first. Abdomen with parallel sides, but not constricted basally ; the quadrate third segment slightly longer than the second, the fourth barely longer than the third ; fifth as long as the second, but rounded apically. Legs simple, the hind femora rather slender. Marginal cell widely open ; third vein straight ; both marginal cross-veins paralleling wing margin ; anterior cross-vein at approximately the basal third or basal fourth of the discal cell ; stalk of first posterior cell moderate ; last section of fourth vein long. The above is taken partly from translation and partly from the figure given by its author ; the species has not been retaken or restudied. The author does not mention sex ; the figure suggests a male, but the eyes are shown widely separated ; it may be dichoptic. By others this genus has been speculatively placed close to *Chrysotoxum*. The venation and simple femora place it, however, almost certainly within the Syrphinae ; the elongate antennae and colour as well as other suggestive features would seem to ally it to *Paragus* ; indeed Arribalzaga mentioned this genus as one of possible relationship. Genotype—*testaceipes* Arribalzaga.

Distribution : neotropical (Argentina) 1.

#### RHODENDORFIA Smirnov.

*Rhodendorfia* Smirnov, *Ent. Mitt.* **13**, 34 (1924).

Face projecting without yellow markings ; facial edge above and below diverging. Eyes bare. Wings broad. Head behind (on the vertex) strikingly strongly

developed; ocelligerous triangle broad, pushed forward. Thorax and scutellum grossly punctate. Abdomen flat; in the female oval, in both sexes very differently coloured: entirely black in the male and prevailing reddish yellow in the female sex. Legs quite simple.

This new genus is closely related to the genera *Platycheirus*, *Pyrophaena* and *Melanostoma*, yet it is distinctly defined from all three. From *Platycheirus* it is distinguished above all by the entirely simple legs and the peculiar abdominal markings, from *Pyrophaena* and *Melanostoma* by the projecting face, noticeably diverging sides of the face and somewhat different abdominal form. From all three it distinguishes itself, moreover: first, by the peculiar build of the head, the strongly-developed posterior region and the broad, forward pressed ocelli; and secondly through the punctate thorax. Genotype—*dimorpha* Smirnov. Related to *Carposcalis* Enderlein.

The above description is a translation of that given by Smirnov.

Distribution: palaearctic 3.

#### CYPHIPELTA Bigot.

*Cyphipelta* Bigot, *Rev. Mag. Zool.* 11, 307 (1859).

A phylogeront. The eyes are large; head little broader than humeri; facets not enlarged. The head is unusually flattened across the top and the eyes are holoptic in the male. The vertical triangle is nearly equilateral. Front and antennal prominence enormously swollen and prominent. First two antennal segments short; third missing. Face below antennae quite concave as far as the first tubercle and then again equally concave to the epistoma. Opposite on either side of these two tubercles there are two bulges. The facial stripes are very wide; wider perhaps than in any other Syrphid. The occiput is well developed below, practically absent above, and the upper eye corners are sharply angulated. The thorax is convex, black, vittate and shining; humeri pilose, scutellum enormously swollen with a very conspicuous flat rim. The abdomen is short, broad, broader than thorax, quickly tapering from the beginning of the third segment and likewise flexed downward from this segment; the posterior part is quite convex and the last two segments largely covered with strange matted appressed pile. The hind femora are a little thickened, they have a double or triple row of short, sharp spinules on the inner and outer sides distally and ventrally. The costa ends before the apex and simultaneously with the third vein; wing pubescent; stigma very long; submarginal cell widely opened. Third vein straight. The apical cross-vein quite long and rather straight. Alulae large and well developed. Squamae rather large. Genotype—*Brachyopa rufocyanea* Walker.

Distribution: Australian (and Tasmania) 1.

#### THE SUBFAMILY CHRYSOTOXINAE.

These are large flies of bright coloration with elongate antennae. They are further characterized by the convex, beaded (emarginate) lateral margins of the abdominal tergites. Like the Syrphinae, to which they show obvious relationship, they have the humeri bare or pubescent in contrast to adjacent pilose areas. It



might be possible to dispose of these flies by uniting them with the Syrphinae. However, there are several reasons for not doing so. In no Syrphinae do we find the front definitely produced out into an elongate antennal process. In the Chrysotoxinae the abdomen is always strikingly convex and oval, so much so that *Dideoides* is scarcely comparable to it. Perhaps *Dideoides* is its closest relation in the Syrphinae. An interesting and more or less unique acquisition is the presence in many species of the angular, projecting posterior corners of the abdominal segments, giving a somewhat shingled effect. The bright lemon-yellow markings on a black background are typical *Syrphus*-like combinations found in the Syrphinae in the greatest exuberance. A few species like *Chrysotoxum violaceum* Brunetti have a wholly dark coloured abdomen, and in *Chrysotoxum rotundatum* the abdomen is round convex. Finally, there is perhaps only the one almost cosmopolitan genus of many species.

#### CHRYSTOTOXUM Meigen.

*Chrysotoxum* Meigen, *Illiger. Magazin. Insektenk.* 2, 275-84, (1803).

Head broadly oval from the front. Eyes holoptic in the male; often densely pilose, sometimes bare. Vertex never swollen; front prominent; antennae quite elongate, all of the segments elongate and all of them slender. Arista about half as long as the antennae in most of the species. Face below the antennae gently concave or practically not at all concave. The face descends, however, to a low conspicuous tubercle but little before the bottom of the eyes, then retreating quickly to the epistoma; from the epistoma the face retreats still farther, for the face is bluntly produced below the eyes. Eyes incised about middle of occiput. Scutellum convex, without rim; metasternum elongate and more convex than any other Syrphid. In a few species the abdomen is subglobose, scarcely longer than wide and still very convex. Sides of the abdomen are always strongly emarginate and in a certain group of species the posterior corners of each segment are shortly, but sharply produced. Abdomen characteristically black, marked with slender, arcuate or straight, sometimes wide bands of brown or even lemon yellow, and frequently narrowed in the middle. The terminal segment bears a variety of patterns. The hypopygium is concealed. The femora and tibiae always slender, the latter nearly as long as femora. Wings elongate, with a long alulae. The apical cross-vein is strongly sigmoid and barely recurrent, joining the third vein remote from apex; third vein and costa ending a little before apex. The marginal angles of the first and second posterior cells may end in conspicuous spurs, and the third vein may be considerably dipped into the first posterior cell, but not kinked. Submarginal cell broadly open. Vena spuria strongly developed. Genotype—*Musca bicinctum* Linnaeus.

Distribution: palaearctic 26; nearctic 23; neotropical 2; Ethiopian 1; oriental 36; holarctic 1.

*Protochrysotoxum* Hull (fossil genus). Characterized by: third vein straight (curved in *Chrysotoxum*). Abdomen very convex. Large flies, with narrow basal abdominal fascia. Anterior cross-vein well before the middle of discal cell. Genotype—*sphinx* Hull. My assignment of this fly here must for the present be something of a guess. Conceivably it might be a *Volucella*, or a *Microdon*.

## THE SUBFAMILY MICRODONTINAE.

The Microdontinae contain a considerable number of characteristic flies of small to large size. In most of the genera the antennae are quite elongate and the elongation is shared by both the first and second segments. But this is often a variable character, and in *Microdon* and *Mixogaster*, where some of the longest antennae are seen, there are some quite short ones. Moreover, the wing venation is characteristic. The apical and postical cross-veins join the third and fourth veins respectively, far back from the wing margin, and the apical cross-vein is often strongly recessive and sometimes recurrent. Finally the lower angles of the first and second posterior cells are often, though not always, broadly rounded. The flies range from pale brownish yellow to red, dark brown, and in numerous cases metallic blue, green or violet. Upon the head the face is fairly uniform and is almost always strongly convex. Rarely is the face straight in profile and never tuberculate or produced downwards. In all the species the eyes are widely dichoptic. The abdomen upon the other hand is immensely variable and ranges from short, compact, convex, subglobose forms, to slender, subcylindrical or strongly petiolate types. It seems apparent that this subfamily is today a rather plastic group of ebullient, florescing forms rapidly evolving, especially in the tropical areas. One of the chief trends seems to be toward the production of numerous, wasp-like, petiolate types, comparable to the Sphegini in the Cheilosinae, and several genera in the Xylotinae. Moreover, the antennae are tending to elongate according to two patterns, and in others to become fissiform.

The Microdontinae are presumably an old group early differentiated from the family. Some Microdontinae wings are not greatly different in some respects from *Sphegina* or *Chrysogaster*, and a possible relationship to the Cheilosinae through *Spheginobaccha* should not be overlooked. A fossil species of *Microdon* has been described from the Tertiary bed of Aix in Provence by Seeres (1829), but the author was not able to find the whereabouts of the type. The habits of the larvae are, as is well known, unique, acting as they do asinquilines in the nests of ants and termites. Such larvae have been collected from the nests found in elder stems in Mississippi.

Perhaps two tribes should be recognized. The first would be the Microdonini distinguished by those genera which usually have an adventitious branch to the third vein emitted into the first posterior cell, and secondly the Ceratophyani, the genera of which never have such a branch.

Of all the genera here placed in the subfamily, probably the one with the most uncertain relationships is *Spheginobaccha*. These flies have usually been put in the Cheilosinae. The author is inclined to the view that in spite of the short antennae and somewhat different wing venation, that these flies are allied to *Paramicrodon* and its relatives. Both of these may be regarded as remote genera. *Spheginobaccha* has the oblique scars upon the hind femora and tibiae seen commonly in this subfamily. Its head, too, is subglobular like *Paramicrodon*. Certainly these flies are aberrant wherever they are placed, with no close relatives now known. Besides this genus the most unique members of the subfamily are *Masarygus* with its furcate antennae, and *Ceriomicrodon*, perhaps a phylogeront.



The following disposition is made of the groups of the subfamily: two tribo-genera; four remote genera including the phylogeronts *Ceriomicrodon* and *Masarygus*; three other genera (*Mixogaster*, *Ubristes*, *Pseudomicrodon*); twenty-seven subgenera. Of these subgenera those of minor importance are: *Dexiosyrphus*, *Tanaopicera*, *Eumicrodon*, *Serichlamys*, *Syrphipogon*, *Myiacerapis*, *Hypselosyrphus*, *Protoceratophya*.

Wheeler erected a neotropical genus *Nothomicrodon*, genotype *aztecarum*, based upon larvae only.

*A key to the groups of the Microdontinae.*

1. Third vein with a downward spur into the posterior cell..... 2  
This vein without an appendix ..... 20
2. Antennae quite short, especially the first and third segments..... *Archimicrodon*, subg. n.  
Antennae elongate and slender, the first and third segments several  
to many times longer than the second ..... 3
3. Abdomen petiolate or constricted or narrowed basally ..... 4  
Abdomen short and compact, the apical segments sometimes  
narrowed and pinched in, but never petiolate, or the abdomen  
narrow and subcylindrical ..... 10
4. The third antennal segment is three to five or more times as long as  
the first ..... 5  
Third antennal segment shorter than first, of the same length, or  
very little longer than the first ..... 6
5. Face straight; third antennal segment six times the length of the  
first and widest subapically and held backwards. Abdomen  
much constricted in the middle of the second segment ..... *Paramixogaster* Brunetti.  
Face convex, the vertex high and prominent; third antennal segment  
little longer than the first, and slightly arched, thick throughout  
except at base and apex. Abdomen very slightly more narrow  
basally ..... *Paramixogasteroides* Shiraki.
6. Abdomen constricted or pinched in between the third and fourth  
segments ..... *Stenomicrodon* Hull.  
The constriction of the abdomen affects much or all of the second or  
of the third segments ..... 7
7. The constriction of the abdomen begins past the middle of the second  
segment, and is largely confined to the third segment; base of  
abdomen wide, flared, flattened, the lateral margins thick and  
rounded. Face rounded and bulging outwardly below. First  
antennal segments especially slender and long, the third lanceolate. *Rhopalosyrphus* Giglio-Tos.  
The constriction of the abdomen is confined largely to the whole  
second segment, or if the third segment is included the head is much  
wider than the thorax ..... 8
8. Abdomen exceptionally narrow, cylindrical and slender on most of  
the second and third segments. Head much wider than the  
thorax, allowing complete and easy inspection of the post-occiput.  
Antennae elongate; apex of abdomen not thrust downward ... *Ceriomicrodon* Hull.  
Abdomen only moderately narrowed, the constriction practically  
confined to the elongate second segment; last three segments of  
abdomen formed into an oval club, strongly flexed downward at  
the end of the second segment. Head of normal width ..... 9

9. Face convex, vertex not greatly developed..... *Pseudomicrodon* Hull.  
 Face nearly straight in profile, the vertex above much enlarged, the eyes reduced ..... *Tanaoplicera*, subg. n.
10. Eyes greatly reduced, the occiput and vertex and cheeks each about as long as the face. Antennae of moderate length; the basally thickened third segment arched and curved ..... *Oligeriops* Hull.  
 Eyes normal; occiput and vertex not so developed ..... 11
11. Hind tibiae and hind basitarsi enlarged, each with strong, thick brushes of hair ..... *Ubristes* Walker.  
 Hind tibiae and femora slender, or slightly thickened basally; pile short, setaceous, normal ..... 12
12. Third antennal segment many times as long as the first and in the male covered on inner and outer sides with dense, very long, erect, soft pile; the base of the segment excavated and in the hollow holding a minute, short fuzz; the arista the same ..... 13  
 Without such pile ..... 14
13. Abdomen short conical, about twice as long as wide; head much wider than the thorax ..... *Ptilobactrum* Bezzi.  
 Abdomen elongate, widest apically. Only three segments visible from above, the fourth, hidden by the shield-like sides of the third, is vertical and appears to be the hypopygium. The hypopygium is concealed and visible only from below ..... *Kryptopyga* Hull.
14. Third antennal segment four to five times as long as first (curved outward and erect) ..... 15  
 Third segment much shorter, not curved outward..... 16
15. Third antennal segment curved outward and erect (bee mimics).... *Myiacerapis*, subg. n.  
 Third segment straight and bulbous at apex ..... *Bardistophus* Mann.
16. Abdomen narrow and nearly cylindrical, the terminal segment rarely a trifle wider than the base, or the second segment widened and flattened ..... *Omegasyrphus* Giglio-Tos.  
 Abdomen short and compact, the base quite wide, flattened, the terminal segments convex and narrowing and somewhat bluntly pointed at apex ..... 17
17. Scutellum very wide, with small spines at each outer posterior corner; two or more times as wide as long; apical cross-vein angularly directed outward, erratic, with or without a spur..... *Eumicrodon* Curran.  
 Scutellum of the usual width; apical cross-vein not angularly directed outward; without a spur ..... 18
18. Scutellum deeply sulcate, almost divided into two lobes; very large flies, the face with a tuft of long bristles just above the epistoma, directed downward ..... *Syrphipogon* Hull.  
 Scutellum semicircular, with or without spines ..... 19
19. Eyes pilose ..... *Serichlamys* Curran.  
 Eyes bare ..... *Microdon* Meigen.
20. Arista composed of three segments, the second longer than the third; apical cross-vein joining third vein near wing apex, its distal half turned outward ..... *Aristosyrphus* Curran.  
 Arista normal, the first two segments hidden or extremely short... 21
21. Abdomen petiolate, the second segment narrow; antennae usually elongate. Occiput never greatly expanded; upward spur of fourth vein into the first posterior cell always present..... *Mixogaster* Macquart.  
 Abdomen with parallel sides, elongate, or sometimes clavate or flattened, oval and broad; occiput sometimes greatly developed and tumid above; spur of fourth vein present or absent ..... 22



22. Head hemispherical or subglobose. Occiput greatly expanded above; antennae quite short, the first two especially short; abdomen slender, often subcylindrical ..... 23  
 Antennae elongate, the first and usually the third joints several to many times longer than wide; abdomen clavate and flattened or oval and flattened ..... 24
23. Occiput with a deep indented crease above on each side; apical cross-vein meeting third vein near apex of wing; abdomen slightly narrowed basally; fourth vein emits an upward spur into first posterior cell ..... *Spheginobaccha* de Meijere.  
 Occiput without such crease; apical cross-vein recessive, no spur from the fourth vein. .... *Paramicrodon* de Meijere.
24. First antennal joint two or more times longer than the second; abdomen widest at the end of the second segment, elongate beyond; fourth and to a lesser extent the third segment of abdomen with deep, wide concave, transverse excavation from margin to margin; hind tibiae and basitarsi with hairy brushes.. *Rhoga* Walker.  
 First antennal segment not greatly longer than the third ..... 25
25. Third antennal segment produced into two enormous bifurcate protuberances. Ocelli sit upon a very high protuberant ocellarium; head very wide and short, abdomen elongate .... *Masarygus* Brethes.  
 Not such flies. Abdomen short and broad and flat, or elongate and flat with parallel sides ..... 26
26. Abdomen elongate, flattened; the sides parallel; hind tibiae and tarsi with normal short pile ..... *Ceratophya* Wiedemann.  
 Abdomen short, oval, flattened; hind tibiae or tarsi or both with brushes of long hairy pile; ocelli somewhat raised; scutellum often triangular ..... *Hypselosyrphus* Hull.

## MICRODON Meigen.

*Microdon* Meigen, *Illiger Magazine Insektenkunde*, 2, 275-83 (1803).

Small to large flies of pallid, metallic, brown, or black coloration with short, compact, convex, or flattened, oval or pointed abdomen. The antennae are always elongate from the first and second segments and the face convex. Eyes of male dichoptic but with an angular approximation near the middle of the front. Eyes bare with rare exceptions. The vertex is only slightly elevated. The ocelli may lie in either an equilateral or isosceles triangle. The scutellum is either equipped with two spines, is sulcate, or its margin entire. The pile, especially upon the abdomen is often appressed. The hind femora are a little thickened; their tibiae are slightly thickened. The cicatrices of both are conspicuous. The hind tarsi are not infrequently greatly enlarged and swollen. The third vein emits a spur into the first posterior cell. Lower corners of first and second posterior cells rounded or angular, with or without appendicular veins. The apical and postical cross-veins are recurrent, sometimes recurrent from their base, and in any case meet their respective veins far back from the wing margin. Genotype—*Musca mutabilis* Linnaeus.

Distribution: palaearctic 16; nearctic 39; neotropical 113; Ethiopian 29; oriental 61; Australian 16; Oceania 1.

Recognized subgenera:

*Eumicrodon* Curran, *Kans. Univ. Sci. Bull.* 15, 50 (1924).

Large metallic, green, compact species with slender, elongate antennae, solely distinguished by the broad, very wide scutellum two to three times as long as wide,

with spines at outer corners. The apical cross-vein may be angulated and have a spur vein, but not always. Subgenotype—*fulgens* Wiedemann

Distribution : neotropical 1 ; oriental 1.

*Serichlamys* Curran, *Kans. Univ. Sci. Bull.* **15** (1923). Based only upon the presence of sparse, faint ocular pile. Based on *Microdon rufipes* Macquart.

*Syrphipogon* Hull, *Psyche*, **44**, 120 (1937).

Very large flies with deeply sulcate scutellum, almost divided into halves. Third and fourth segments with deep, oblique, excavated furrows. The convex face has a tuft of stiff, downwardly directed bristles above epistoma. Subgenotype—*fucatissimus* Hull.

Distribution : neotropical 1.

*Omegasyrphus* Giglio-Tos., *Boll. Mus. Zool. Anat. Comp. Torino*, **6**, 108 (1891).

A small group of *Microdons* distinguished only by the fact that the abdomen beyond the second segment is narrowed and cylindrical, and a little more elongate. The second segment is widened, flattened, flared, its lateral margins subcircular, thickened, rounded. Antennae of only moderate length. Subgenotype—*Microdon coarctatus* Loew.

Distribution : nearctic 3 ; neotropical 2.

*Chrysidimyia* Hull, *Psyche*, **44**, 116 (1937).

Face bulging and prominent below, the antennae arising from a short shelf-like extension of the front. Abdomen about twice as long as wide with parallel sides, the apex rounded. Head and thorax and abdomen with deep sunken pits. Brilliant blue-green species which are remarkable mimics of the cuckoo bees. Subgenotype—*chrysidimima* Hull.

Distribution : neotropical (Brazil) 2.

*Bardistophus* Mann, *Ann. Ent. Soc. Amer.* **13**, 61 (1920).

Dark-coloured *Microdon*-like flies with broad, short abdomen, in which the third antennal segment is very elongate, and the face is straight in profile. The third segment of the antenna is about fifteen times as long as the second, which is almost one-fourth as long as the first. The base of the third segment is slightly bulbous and the segment is expanded from the narrow neck towards the pointed apex. The arista is quite short and thickened. The whole facies of this fly must be somewhat similar to *Microdon pachystylum* ; yet it is doubtful if it is related. Subgenotype—*papuanum* Mann.

Distribution : Oceania (Solomon Is.) 1.

*Myiacerapis*, new subgenus.

Elongate, *Microdon*-like flies in which the terminal segment of the abdomen is much narrowed, is two and a half times as long as the third segment, and in which the third segment of the antennae is four or five times as long as the first and curved and erect. The arista is about half the length of the second segment. Face convex. Front of male unusually broad, the eyes bare. Venation like *Microdon*. Subgenotype—*Microdon villosus* Bezzi.

Distribution : Ethiopia 1.



*Ptilobactrum* Bezzi, *The Syrphidae of the Ethiopian Region*, 136 (1915).

Remarkable flies, in general like *Microdon*, with short, bluntly conical abdomen, and with the very long third antennal segment covered on lateral and medial surfaces with quite long, thick, erect soft pile. The base of the segment is excavated and there bears a minute, shortened, thickened lanceolate arista. Bezzi had only the male. His figure is marked female, but this is an error. The author saw and illustrated a female now in the British Museum. In this sex the third segment bears only short, thick fuzz; the arista is similar to the male. The venation is like that of *Microdon*, the lower angles of first and second posterior cells sharp, acute and spurred. The head is considerably wider than the thorax. Thus it will be seen that this fly differs in only one real particular from *Microdon*; it is analogous to *Copestylum* in the Volucellinae. Subgenotype—*neavei* Bezzi.

Distribution: Ethiopian 1.

*Ubristes* Walker, *Insecta Saundersiana. Dipt.* 1, 217 (1852).

These are flies in which the rather thinned, somewhat flattened abdomen is more or less elongate, though not narrowed or petiolate. They are often pallid in coloration, or dark brown. The principal characteristic is the greatly thickened hind femora, tibiae, and basitarsi, which bear long, thick brushes of pile. These are the *Trigona* bee mimics. The antennae are moderately elongate. In the genotype the third vein has a well-developed spur vein, yet there seems an obvious relation to such genera as *Rhoga* Walker, *Ceratophya* Wiedemann, *Hypselosyrphus* Hull, all of which lack this vein. It is possible that several phyletic lines have independently lost or are in process of losing this appendiculate vein. Genotype—*flavitibia* Walker.

Distribution: neotropical 4.

*Kryptopyga* Hull, *J. Wash. Acad. Sci.* 34, 129 (1944).

Flies with elongate abdomen, the apex barely wider than the base. The third segment in the male appears to be the terminal segment, which reaches down and encloses by its lateral shield-like margins the fourth segment, directed vertically downward, which appears to be the hypopygium. The true hypopygium can only be seen from below. The antennae are exceptionally elongate, the third segment being many times longer than the second; its pile, however, is not remarkable. The arista is minute and lanceolate as in *Ptilobactrum*. Female unknown. Genotype—*pendulosa* Hull.

Distribution: oriental 1.

#### OLIGERIOPS Hull.

*Oligeriops* Hull, *Psyche*, 44, 26 (1937).

Small species, the abdomen about twice as long as wide with rounded apex. On the head the eyes are greatly reduced and as a consequence the vertex, front, occiput and cheeks are as thick and long as the face. The moderately elongate antennae have a peculiar third segment. It is basally thickened, arched and curved, or excavated dorsally; arista short, legs simple, venation *Microdon*-like. Genotype—*Microdon chalybeus* Ferguson.

Distribution: Australian 1.

## PSEUDOMICRODON Hull.

*Pseudomicrodon* Hull, *Psyche*, **44**, 24 (1937).

These are the flies which are counterparts in many respects of *Mixogaster*, but which possess a well-developed appendiculate vein from the third vein, directed into the first posterior cell. The antennae are elongate. Face convex, abdomen, to a much greater extent than *Mixogaster*, is flexed characteristically downward at the end of the second segment, the last two or three segments semi-fused into an oval club. The second segment is apt to be marked with hyaline spots. Venation *Microdon*-like. Genotype—*beebei* Curran.

Distribution : Ethiopian 1 (*illucens* Bez.); neotropical 2.

Recognized subgenera : *Tanaopicera* Hull, *Proc. N. Eng. Zool. Cl.* **23**, 76 (1945).

This name is presented for a species with straight face, and greatly developed vertex. Antennae, wings and abdomen like *Pseudomicrodon*. The fore femora are strongly bent and distorted at the pronounced femoral cicatrix. Subgenotype—*Ceratophya variegatus* Walker.

Distribution : Australian 1.

## PARAMIXOGASTER Brunetti.

*Paramixogaster* Brunetti, *Fauna Brit. India*, Dipt. **3**, 320 (1923).

These flies with the second abdominal segment considerably constricted, with nearly parallel sides. Apex of abdomen club-like. The antennae very elongate; third segment gradually widening to near its apex, six times as long as the first segment. Second segment minute. Third vein with appendiculate spur. Genotype—*vespiformis* Brunetti.

Distribution : oriental (Assam) 1. Brunetti calls the antennae absolutely bare, but does not indicate if pubescence is also wanting.

## PARAMIXOGASTEROIDES Shiraki.

*Paramixogasteroides* Shiraki, *Mem. Fac. Sci. Agric. Taihoku*, **1**, 8 (1930).

Slender flies, the base of the abdomen barely more narrow than the apex. The antennae are only moderately elongate, but the third segment is somewhat thickened and curved dorsally, its base and apex attenuated. Genotype—*Myxogaster variegata* Sack.

Distribution : palaearctic (Formosa) 1.

*Stipomorpha* Hull (subgenus), *Proc. N. Eng. Zool. Cl.* **23**, 74 (1945).

*Microdon*-like flies with the first two abdominal segments greatly flared and flattened and wider than the thorax; remainder of abdomen immediately compressed into a rounded, subcylindrical, pipe-like form. Subgenotype—*fraudator* Shannon.

Distribution : neotropical 1.

*Parocyptamus* Shiraki, *Mem. Fac. Sci. Agric. Taihoku*, **1**, 11 (1930).

*Stenomicrodon* Hull, *Psyche*, **44**, 26 (1937).

Slender, quite elongate species, which most resemble the American subgenus *Omegasyrphus* in some respects. The first and second segments of the antennae are



moderately elongate. The first segment of the abdomen is flattened; its lateral margins are not convex. In both males and females there is a very pronounced anterior plate at the base of the first four femora, covered with very stiff, dense, long setiferous, reddish bristles, much more pronounced than the stiff patches of pile seen on some other *Microdons*. In the form to which I gave the name *Stenomicrodon* and which may be the same as *Parocyptamus*, the abdomen (female) is strongly pinched in between the second and third segments, and less so between the third and fourth. *Microdon stenogaster* Curran evidently belongs here. Subgenotype—*sonami* Shiraki.

Distribution; palaearctic (Formosa) 1; oriental (Borneo) 1. Shiraki was mistaken in supposing this fly to be related to *Oyptamus*, a species group of *Baccha*.

*Archimicrodon* Hull (subgenus), *Proc. N. Eng. Zool. Cl.* **23**, 75 (1945).

These are *Microdon*-like flies in which the antennae are quite short, and not much longer than in some species of *Syrphus*. There appear to be a number of such species in the Australasian region. Face convex, venation *Microdon*-like. These flies seem to approach much more closely to the archaic type than any of the typical palaearctic or occidental *Microdons*, with their long slender antennae. Genotype—*Microdon digitator* Hull.

Distribution: oriental (Java) 1; Australian several.

#### RHOPALOSYRPHUS Giglio-Tos.

*Rhopalosyrphus* Giglio-Tos, *Boll. Mus. Zool. Anat. Comp. Torino*, **6**, 108 (1891).  
*Holmbergia* Arribalzaga, *Ann. Soc. Cien. Argent.* **32**, 195 (1891).

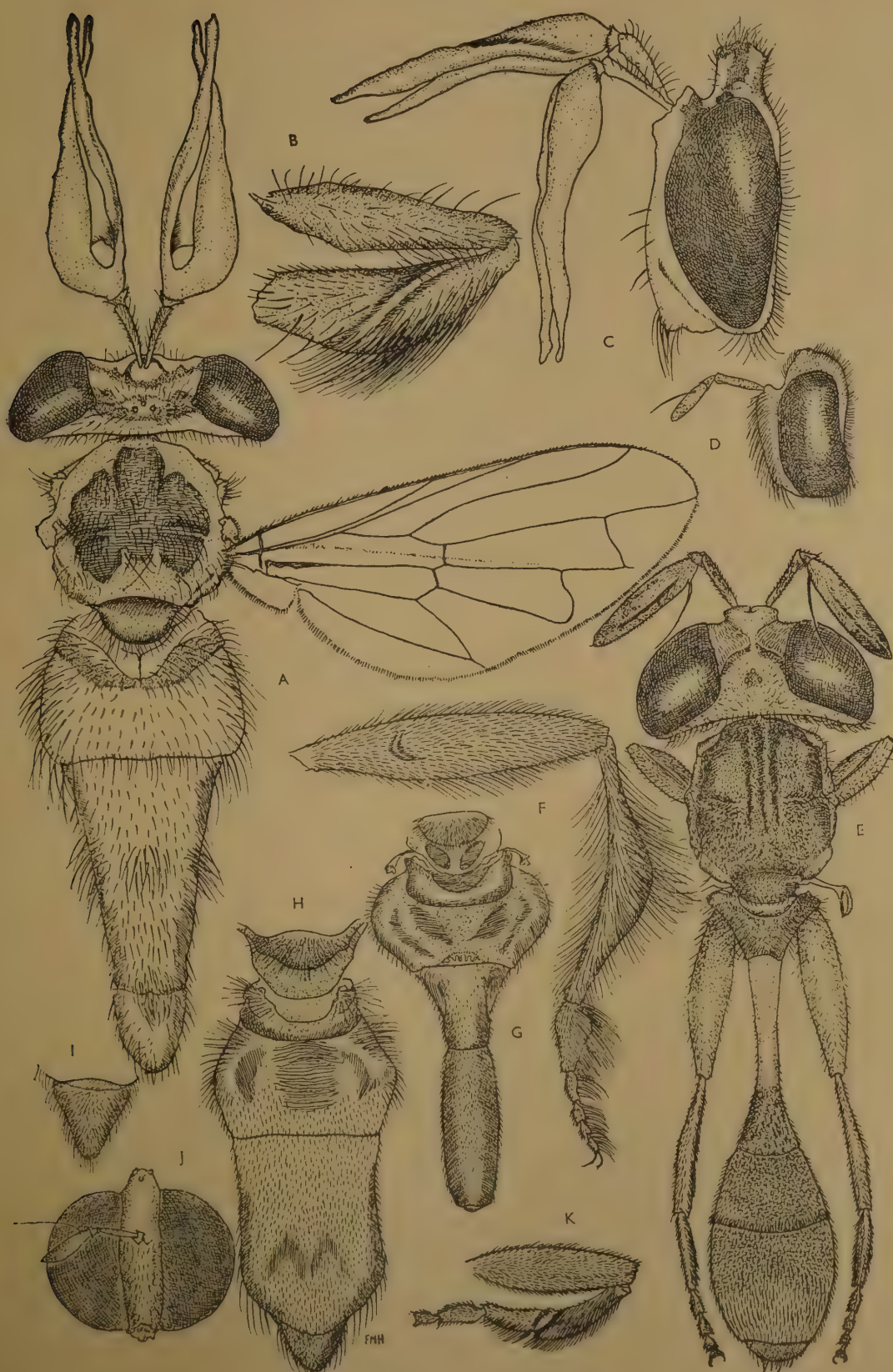
Slender, petiolate flies, the last segments club-like and the first and second rather wide and flared and flattened. The intervening area is cylindrical. The face bulges outward below, leaving the upper half shallowly concave. The antennae are quite elongate, and the segment particularly narrow and slender; third elongate-lanceolate. Legs simple. Venation typical; third vein with appendiculate vein. Genotype—*Holmbergia guntherii* Arribalzaga.

Distribution: neotropical 2. It remains to be seen if Giglio-Tos' Mexican species is the same that Arribalzaga had from Argentina. Sack has described one from Paraguay.

#### The Subfamily Microdontinae.

- A. *Masarygus megacephala* Shannon, dorsal view (holotype); B. *Masarygus megacephala* Shannon, hind femur and tibia (holotype); C. *Masarygus megacephala* Shannon, profile of head; D. *Hypselosyrphus scutellaris* Shannon, profile of head (type); E. *Ceriomicrodon poliolatus* Hull, dorsal view (holotype); F. *Ubristes flavitibia* Walker, hind femur and tibia (type); G. *Stipomorpha fraudator* Shannon, abdomen (type); H. *Ubristes flavitibia* Walker, abdomen (type); I. *Hypselosyrphus scutellaris* Shannon, scutellum (type); J. *Hypselosyrphus scutellaris* Shannon, front view of head (type); K. *Hypselosyrphus scutellaris* Shannon, hind femur and tibia (type).

Fig. 13.





## CERIOMICRODON Hull.

*Ceriomicrodon* Hull, *Psyche*, **44**, 25 (1937).

A phylogeront. These are unusual flies, with petiolate abdomen, fully as slender as some Cerioidinae. The base and apex are expanded, but the latter is held out straight and not flexed downward. The antennae are elongate. The head however is so much wider than the thorax that every detail of the post-occiput can be readily inspected. Scutellum unspined. Legs simple. Venation *Microdon*-like with appendiculate vein attached to the third vein. Genotype—*petiolatus* Hull.

Distribution: neotropical (Brazil) 1.

## MIXOGASTER Macquart.

*Mixogaster* Macquart, *Dipt. Exot.* **2**, Pt. 2, 14–15 (1842).

Slender, petiolate species with elongate antennae, of variable length, and with the apex of abdomen club-shaped. Scutellum unspined. Legs simple, venation characteristic; as delimited today the genus is restricted to those species which completely lack the appendiculate spur from the third vein. There is a characteristic short stump vein emitted by the fourth vein near its end, upward into the first posterior cell. Thus *Mixogaster* is, according to the author, derived from *Pseudomicrodon*. However, it is possible that these two genera have secured the form of their abdomen by parallel development and convergence. Genotype—*conopsoides* Macquart.

Distribution: nearctic 3; neotropical 14.

## CERATOPHYA Wiedemann.

*Ceratophya* Wiedemann, *Analecta Entom.* **14** (1824).

These are elongate, but rather flattened, thinned, and not slender species of *Microdon*. The antennae are elongate but the venation is characteristic in lacking the appendiculate vein from the third vein into the first posterior cell. Apical cross-vein recurrent. Genotype—*notata* Wiedemann.

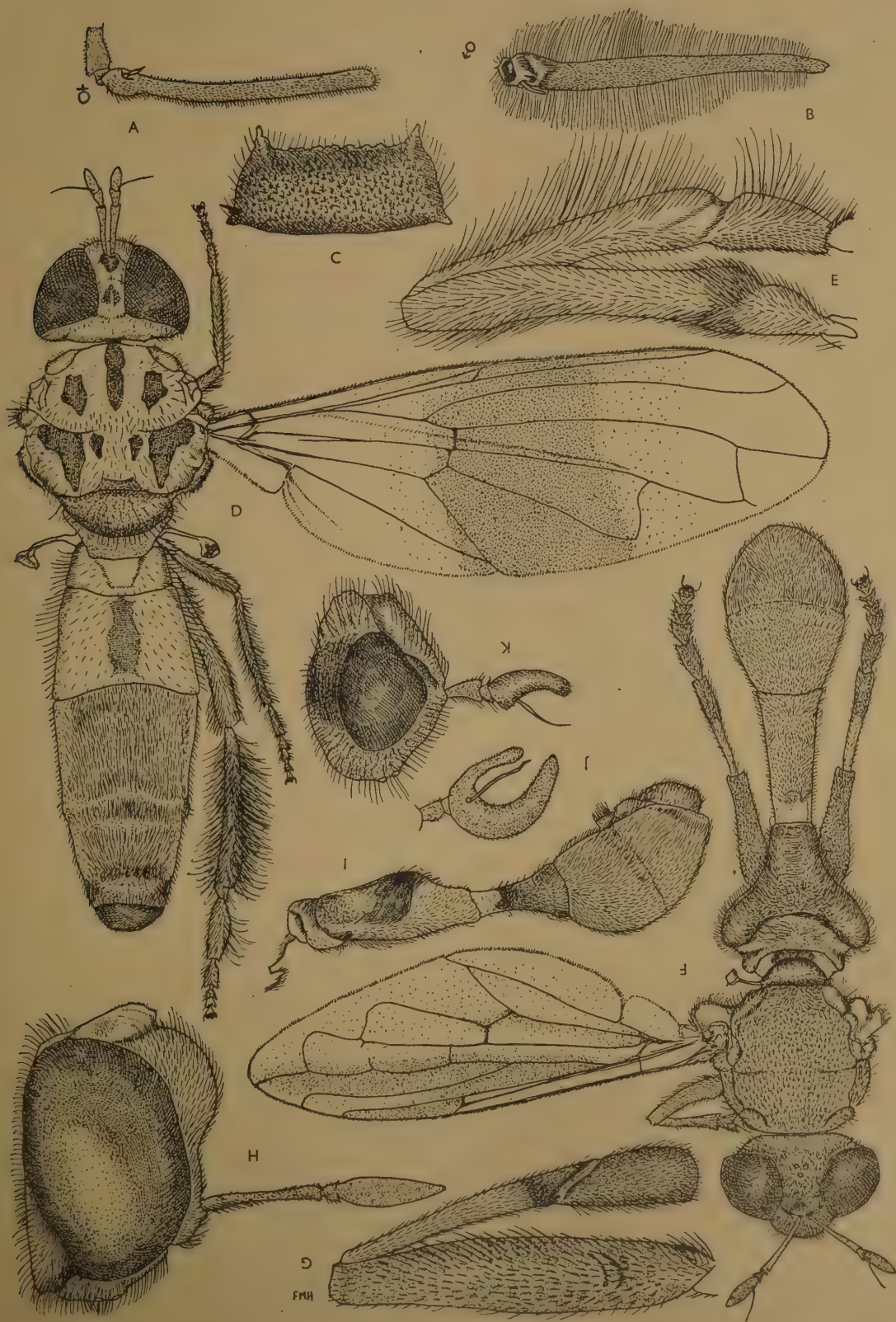
Recognized subgenera: *Protoceratophya*, new subgenus, for those species in which the last half of the apical cross-vein joins the third vein at a sharp angle near the apex of the wing. Subgenotype—*carpenteri* Hull.

Distribution: neotropical 9. *Ceratophya macroptera* Curran with its trituberculate face should probably have subgeneric rank.

## The Subfamily Microdontinae.

- A. *Ptilobactrum neavei* Bezzi, antenna of female; B. *Ptilobactrum neavei* Bezzi, antennae of male (type); C. *Eumicrodon fulgens* Wiedemann, scutellum; D. *Rhoga sepulchrasilva* Hull, dorsal view; E. *Rhoga sepulchrasilva* Hull, hind femur and tibia; F. *Rhopalosyrphus guntherii* Arribalzaga, dorsal view; G. *Rhopalosyrphus guntherii* Arribalzaga, hind femur and tibia; H. *Rhopalosyrphus guntherii* Arribalzaga, profile of head; I. *Rhopalosyrphus guntherii* Arribalzaga, lateral view of abdomen; J. *Cervicorniphora alcornis* Ferguson, antenna (redrawn from Ferguson); K. *Oligeriops chalybeus* Ferguson, profile of head.

Fig. 14.





## ARISTOSYRPHUS Curran.

*Aristosyrphus* Curran, *Bull. Amer. Mus. Nat. Hist.* **78**, 252 (1941).

A *Ceratophya*-like fly with a very peculiar arista. The first segment is short, but the second is greatly elongate and even larger than the third. I have seen the genotype. Curran remarks that the condition of the arista is duplicated in the Muscoids. Subgenotype—*primus* Curran.

Distribution : neotropical (Brazil) 1.

## RHOGA Walker.\*

*Rhoga* Walker, *Trans. Ent. Soc. Lond.* **4**, 157 (1857).

*Papiliomyia* Hull, *Psyche*, **44**, 27 (1937) for *sepulchrasilva* Hull.

These are small species of pallid, yellowish coloration, the wings yellowish and banded with grey. The abdomen is a little more than twice as long as wide, flattened basally, a little narrowed apically, and has prominent, wide, transverse curved excavations upon the third and fourth segments. The vertex is protuberant, and the antennae are situated near the top of the head. The antennae are characteristic in that the first segment is quite long and about twice as long as the first and second segments combined. The face is narrower than the front, converging below. Eyes bare and very large, covering most of the head, the cheeks practically absent. The face convex in profile. The hind femora are slender but the hind tibiae are thickened apically with a deep shallow groove. The hind tibiae have a pronounced brush as in *Ubristes*. The weak, delicate wings lack the appendiculate vein into the first posterior cell. The species slightly suggests moths or scorpion flies and perhaps inhabit very dark forests. Genotype—*lutescens* Walker.

Distribution : neotropical 4.

## MASARYGUS Brethes.†

*Masarygus* Brethes, *An. Mus. Nac. B. Aires*, **3**, 442 (1908).

Unique flies in respect to the greatly developed fissiform third antennal segment. Pallid, yellowish flies, the abdomen elongate, a little narrowed apically and the face quite straight in profile, with epistomal bristles. The hind femora as well as the hind tibiae, are greatly thickened, and equipped with thick brushes of pile. The venation is like *Rhoga*. The antennae are elongate, the third segment large and deeply cleft so as to have quite elongate prongs; the cleft reaches almost to the base. This style of antennae more or less is duplicated among the fissicorn

\* *Eurypterosyrphus* has been erected by Baretto and Lane, with *melanopterus* as genotype (Brazil), in *Rev. de Entomologia*, vol. 18, page 141 (1947). This is a weakly characterized group, differing from *Rhoga* in minor respects of face shape, frontal prominence, non-ciliate hind tibiae, etc. The villosity of the wing and shape of the costal cell, etc., do not deserve great weight. It may be regarded as a subgenus of *Rhoga*.

† The following genera recently erected appear to be synonyms of *Masarygus* :

*Schizoceratomyia* Carrera, Souza-Lopes and Lane, with *barreto*, sp. n., in *Brazil-Medico*, vol. lxi, 3, July 1947. Also *Johnsoniodon* Curran, with *malleri*, sp. n., in *Amer. Mus. Novitates*, No. 1347, July 1947.

Tachinidae by *Dichocera*. This author would regard *Masarygus* as a *Rhoga* with fissicorn antennae. Genotype—*planifrons* Brethes.

Distribution : neotropical 2. I place here also *Microdon megacephalus* Shannon, which I have figured. While there are some differences, and the third segment of this species is far longer and more extravagant than the genotype, the author sees no real distinction.

#### HYPSELOSYPHRUS Hull.

*Hypselosyrphus* Hull, *Psyche*, **44**, 21 (1937).

Small brown flies, with very convex face, exceptionally narrow face and very protuberant vertex. The antennae are elongate, the first and third segments equal in length, the latter narrowly oval. Scutellum thick and deeply sulcate, or in some species elongate, quite triangular and pointed and directed upwards as in certain Stratiomyids. Hind tibiae and their basitarsi greatly swollen, the former with a curious crease ; no brushes of pile. The third vein has no appendiculate vein ; marginal cross-veins straight. Genotype—*trigonus* Hull.

Distribution : neotropical ; two or three species.

#### CERVICORNIPHORA Hull.

*Cervicorniphora* Hull, *Proc. N. Eng. Zool. Cl.* **23**, 75 (1945).

Small, *Microdon*-like flies in which the third antennal segment is deeply cleft into two prongs, widely separated. The third vein has the appendiculate branch into the first posterior cell. Subgenotype—*Microdon alcicornis* Ferguson.

Distribution : Australian 1.

#### PARAMICRODON de Meijere.

*Paramicrodon* de Meijere, *Nova Guinea*, **9**, 360 (1913).

*Syrphinella* Hervé-Bazin, *Encyl. ent.* (B) **2** ; Dipt. **3**, 73 (1926).

*Myxogasteroides* Shiraki, *Mem. Fac. Sci. Agric. Taihoku*. **1**, 9 (1930).

Based on *Mixogaster nigripennis* Sack. Identical as far as head and wings are concerned.

A remote genus. These are small flies in which the abdomen is slender and subcylindrical, and rounded immediately near the apex. The third vein lacks the appendiculate vein and the marginal cross-veins are straight and meet their veins more or less rectangularly. The legs are rather simple. The hind femora are slightly thickened, but because the base is attenuated and spindly, they appear more so. These flies are peculiar in the subglobose head. The occiput is well developed behind the ocelli but gradually thins until negligible below. The face is narrow with parallel sides and convex and short in profile. The eyes are bare and quite large. The antennae are very short ; the first and second segments are subequal and short, and the third elongate oval, about as long as the first two together. Genotype—*lorentzi* de Meijere.

Distribution : oriental ; five or six species have been described from the East Indies.



## SPHEGINOBACCHA de Meijere.

*Spheginobaccha* de Meijere, *Tijdschr. Ent.* **51**, 327 (1908).

A remote genus. Slender flies, the abdomen somewhat narrowed near the middle, with very short antennae and globose head. The much thickened occiput has a characteristic deep crease in the lateral aspect along the eye margin near the upper third. Eyes bare, narrowly holoptic or dichoptic. The face is convex or straight, and then retreating below. The third antennal segment is but little longer than wide, the first two deeper than long. Scutellum simple. Hind femora rather slender, a little thickened throughout except upon the spindly attenuated base. There is a transverse submedian scar on hind femora and tibiae. The tibiae are compressed or pinched in subapically. The venation is rather suggestive of *Baccha*, or of *Brachyopa*. The fourth vein emits an upward spur near its end into the first posterior cell as in *Mixogaster*. The small cross-vein is before the middle of the discal cell, at about the upper third. Genotype—*Sphegina macropoda* Bigot.

Distribution: oriental 2; Ethiopian 1.

Recognized subgenera: *Dexiosyrphus* Hull. Spur from fourth vein virtually absent; mesonotum with deep crease across the middle connecting the two sutures. Subgenotype—*funeralis* Hull.

Distribution: Ethiopian 1.

*Nannomyrmecomylia* Hull (subgenus), *Proc. N. Eng. Zool. Cl.* **23**, 75 (1945).

I do not believe that *Paramicrodon delicatulus* Hull, described from Cuba, is congeneric with *Paramicrodon*, though its general relationship is obvious. They are very small subcylindrical flies of about 8 mm. length. The second abdominal segment is flattened, the second and third emarginate, the apex of the abdomen slightly wider than the base. Sides of abdomen very deeply curled over apically. Subgenotype—*delicatulus* Hull. *Microdon flukei* Curran, which that author has recently placed in *Ceratophya*, and *Microdon gracilis* Bigot, from Mexico, may both possibly belong here.

## NOTHOMICRODON Wheeler.

*Nothomicrodon* Wheeler, *Proc. Nat. Acad. Sci.* **10**, 243 (1924).

This name was erected for peculiar Microdontine larvae from Panama. The genotype was given as *aztecarum*, sp. n.

## THE SUBFAMILY EUMERINAE.

The Eumerinae wing and that of *Microdon* resemble each other very closely, and there are many other things in common about these two groups of flies, in spite of the fact that the antennae of the one are almost never short, and the antennae of the other are almost never long. *Nausigaster*, too, must be related to *Eumerus*. Its resemblances will be noted under that subfamily, but its apical cross-vein is not spurred.

The Eumerinae contain only five recent groups and it is noteworthy that these flies are practically confined to southern Europe, Africa and Asia. There are a few in Australia. Nowhere do they occur in the new world, save as they have been

introduced by commerce. Still, if none of these occur in the new world, there is yet a subfamily which probably replaced them there. This is the aridophilous genus *Nausigaster*, the habits of its larvae unknown. If not actually a bulb feeder like *Eumerus* or a myrmecophile-like *Microdon*, they must have very interesting habits indeed. With *Eumerus* regarded as a tribogenus, two subgenera *Amphoterus* and *Megatrigon*, and one genus *Azpeytia* are recognized by the author. In addition the fossil fly *Doliomyia* is placed here.

*A key to the groups of the Eumerinae.*

1. Apical cross-vein with a sharp outward bend ; usually with an outwardly directed spur vein straight or rarely with a slight dip.... 2  
     Apical cross-vein rounded distally, the third vein with a well-developed kink ; distal part of the first posterior cell beyond the loop, quite long. Face slightly retreating. Eyes holoptic ; pilose. Scutellum almost as wide as the thorax, about three times as wide as long, with a marginal furrow and crenulate rim. *Azpeytia* Walker.
2. Apical cross-vein with a well-developed outward spur, the distance between postical and apical cross-veins about as long as the last section of the latter. Occiput not with rectangle ..... 3  
     Apical cross-vein with a rectangular bend but without spur. Distance between postical and apical cross veins short. Occiput exceptionally thick and tumid, its margin or rim nearly rectangular..... *Megatrigon* Johnson.
3. Antennae elongate, especially the second segment which is about five times as long as the third ; hind femora simple ..... *Amphoterus* Bezzi.  
     Antennae short..... 4
4. Hind femora simple, the distal third with six to eight denticulate spines ventrally ..... *Eumerus* Meigen.  
     Hind femora massive, with teeth, or teeth and flange-like plate distally and ventrally ..... *Eumerus* Meigen.

*EUMERUS* Meigen.\*

*Eumerus* Meigen, *Syst. Beschreibung*, 3, 202 (1822).

*Citibaena* Walker, *Proc. Linn. Soc. Lond.* 1, 124 (1857).

Small, dark, or often metallic flies, seldom relieved by spots of lighter colour. The eyes are pilose or bare, usually but not always holoptic in the male to a greater or less degree. Face straight, the oral margin rounded, or the face may be retreating or concave and retreating. Antennae short ; third segment often truncate apically or subtriangular. Scutellum usually with thinned emarginate rim ; sometimes minutely denticulate. Abdomen about twice as long as wide, moderately flattened, the segment often transversely excavated or bullose. Hind femora greatly thickened in the genotype and in most species, and spinose denticulate ventro-distally. The degree of thickening varies to some extent. Some species have a plate-like flange on the outer part of the femora. Venation with angulated apical cross-vein, usually with spur, the last section strongly recurrent. Genotype—*Eumerus strigatus* Fallen.

Distribution : palaearctic 60 ; Ethiopian 33 ; oriental 38 ; Australian 7 ; Oceania 3 ; (2–3 species introduced into the nearctic region).

\* *Doliomyia* Hull (1945), p. 328. A fossil genus closely related to the Recent Genus *Eumerus*. It is distinct in the form of face, slender unspined hind femur and bare eyes. Genotype—*chalybea* Hull.



Fig. 15.



## The Subfamily Eumerinae.

- A. *Azpeyia scutellaris* Walker, dorsal view; B. *Azpeyia scutellaris* Walker, profile of head; C. *Eumerus strigatus* Fallen, hind femur and tibia; D. *Eumerus strigatus* Fallen, wing; E. *Azpeyia scutellaris* Walker, hind femur and tibia; F. *Megatrigen sexfasciatus* Johnson, wing (type); G. *Megatrigen sexfasciatus* Johnson, hind femur and tibia (type); H. *Megatrigen sexfasciatus* Johnson, profile of head (type); I. *Amphoterus cribratus* Bezzi, profile of head (type); J. *Eumerus strigatus* Fallen, profile of head; K. *Ciitbaena ergator* Hull, hind femur and tibia.

*Megatrigen* Johnson, *Proc. Acad. Nat. Sci. Philad.* 159 (1898).

These are *Eumerus*-like flies in which the occiput is especially tumid and thick with nearly rectangular margin. The apical cross-vein is recurrent and bent at a right angle and has no spur. The distance between the postical and apical cross-vein is short. Subgenotype—*sexfasciatus* Johnson.

Distribution : Ethiopian 1.

*Amphoterus* Bezzi, *The Syrphidae of the Ethiopian Region*, 116 (1915).

*Eumerus*-like flies with pilose, dichoptic eyes in which the antennae are quite elongate. The second antennal segment is especially long, about six to eight times as long as the first; third segment four-fifths as long as second. The hind femora are simple. The venation is characteristically Eumerine, with an outward spur to the apical cross-vein at its angular bend; last section sharply recurrent. Subgenotype—*cribratus* Bezzi.

Distribution : Ethiopian (Br. E. Afr.) 1.

#### AZPEYTIA Walker.

*Azpeytia* Walker, *Proc. Linn. Soc. Lond.* 8, 113 (1865).

An aberrant Eumerine, somewhat larger than usual. Dark in coloration with short antennae in which the third segment is dorsodistally truncate but rounded. Face retreating, with a slight epistomal eminence; eyes holoptic. Scutellum remarkably wide, some three times as wide as long, the trench-lined, emarginate rim of the scutellum strongly crenulate. Hind femora only a little thickened. Venation distinct; third vein with a rounded kink; apical cross-vein rounded into right angled, unspurred bend which is sharply recurrent; apical portion of first posterior cell long. Genotype—*scutellaris* Walker.

Distribution : oriental 6.

*Palaeopipiza* Meunier (fossil genus). Characterized by : face flat, the epistoma little produced; hind femora short and slender. Third vein convex, the second and third quite divergent apically. Both marginal cross-veins straight, the postical cross-vein oblique and joining the fourth vein remote from the base of apical cross-vein; stalk of first posterior cell short. Genotype—*xenos* Meunier.

#### THE SUBFAMILY NAUSIGASTERINAE.

The *Nausigasters* are small but remarkable flies which mimic the Chrysididae. They are characterized by a subglobular head with large eyes and swollen, broadly rounded face. The antennae are very short and placed at or below the middle of the head. The surface of the fly tends towards pollinose and shows profound puncturation; the scutellum is thin-rimmed, pollinose and subdentate. There is a tendency towards a cylindrical drooping abdomen. The hind femora are thickened. The apical cross-vein of the wing is rounded rather than acutely bent angularly outward; instead of an outward spur, there may be an inner one. Moreover the cross-vein is not truly recurrent.

All of these characters strongly suggest the Eumerinae, with the exception of the form of the apical cross-vein. The face of *Nausigaster* is microtuberculate; in



*Eumerus* it ranges from slightly concave to slightly convex, never tuberculate. There is only the one genus. However, I believe there is a comparatively close relationship here between these ground-loving, low-flying, arid country species and the old-world Eumerinae whose larvae live in bulbs. The cylindroid abdomen is carried to an extreme in *Nausigaster*, which might almost be described as armoured. The terminal part is rounded and smoothed off into a quite cylindrical, fused body with dome-like tip. On the ventral posterior edges the lips of flared chitinous edges reminding one of Chrysids. Matsumura has described a genus *Nephomyia* from Japan, said to resemble *Nausigaster*; it has not been seen by the author.

#### NAUSIGASTER Williston.

*Nausigaster* Williston, *Trans. Amer. Ent. Soc.* **11**, 33 (1884).

A remote genus. The head is subglobular, comprised mostly of the eyes, which are usually bare. Eyes holoptic in male. The vertical triangle is almost confined to the ocelli, which are scarcely raised above the surface. Front very short; antennae placed at the junction of the upper and the middle third of the head; first two segments excessively short; third quite large, thick and orbicular. The quite short arista is placed to one side and some distance out toward the end of the segment. Face below the antennae rather deeply concave, thence rising to a conspicuous obtuse tubercle and quickly retreating to the epistoma, which is barely produced enough to be noticeable, so that the face is nowhere much produced. Cheeks inconspicuous. Occiput everywhere tumid and conspicuous. Face and front pilose. The thorax scarcely elongate, rather convex, the humeri reduced. The dorsum of the thorax and its pleura are evenly continuous with one another and fused along a sutural crease. Scutellum more than twice as broad as long, the margin quite thinned and nodulate. The abdomen is very convex; subcylindrical; the sides curl over strikingly; four segments are visible and the last two are almost as long as the first; three are fused as in *Microdon*. First segment short. The abdomen is widest at the base of the second segment and is somewhat shorter at the end of this segment; from there on the sides are nearly parallel, tapering but little to the middle of the last segment, where it tapers quickly to a rounded end. Sides of abdomen with a strongly emarginate crease, ending at the tip with odd little lobes, suggestive of a cuckoo bee. Abdomen drooping from base and itself flexed only from end of second segment, where there is a deep crease; hypopygium quite concealed and sheltered. The hind femora are short, but little thickened; hind tibiae slender and bent, scooped out dorsodistally; hind basitarsi enlarged. On the wings the subapical cross-vein is kinked in the middle, joining third vein nearly at tip of wing and acutely. Third vein and costa end just before the tip. The angles of the first and second posterior cells without spurs, the latter rounded, the marginal cell is open, the second vein turning sharply to join the costa at right angles. A stigmal cross-vein is present. Vena spuria well developed before the small cross-vein, which is set just before the middle of the discal cell. Alula well developed. Wing usually with one or more clouded spots at the middle or apex or both. This is a small, well-formed genus, of small compact flies which are usually

metallic and tend to parallel the cuckoo bees in some respects. Genotype—*punctulata* Williston.

Distribution : nearctic 8 ; neotropical 6.

#### THE SUBFAMILY CHEILOSINAE.

The flies of this large subfamily are typically dark, often metallic, small, pilose species of sombre coloration. A few genera tend to be relieved by lighter coloration as in *Sphegina* and *Brachyopa*. The subfamily is characteristically holartic in distribution and about seventy-two per cent. of the known species are found in Europe and the nearctic region. As many as forty fossil species are known ; these are distributed among six Recent genera and twelve fossil genera or subgenera. Twenty-six of these species are from the Baltic amber.

The taxonomic arrangement of this subfamily is by no means simple. It shows marked relationship with the Volucellinae on the one hand, through *Ferdinandea* and the plumose Chilosini and with Xylotinae upon the other, through *Myiolepta*, *Odyneromyia*, etc. *Ceriogaster*, now of the Xylotinae, was once placed in the Cheilosinae and there is marked resemblance to *Cynorhina* by *Chalcomyia* and to *Xylota* by *Hemixylota*. It is very difficult still to draw lines between the Cheilosinae and the Xylotinae that are at all convincing or satisfactory. *Ferdinandea* shows the following resemblances to *Volucella* : (1) metallic colour ; (2) prominent bristles ; (3) numerous radial sector bristles ; (4) not greatly dissimilar face. If the arista were plumose, the venation would be the only distinguishing character that remained. The Cheilosinae characteristically have the small cross-vein before the middle of the discal cell, rarely at or just before the middle.

The author recognizes six tribes, everyone of which is represented by fossil species as far back as the Oligocene. (1) The Rhingini are easily distinguished and are ancient ; (2) The Pipizini ; here the face is concave in both sexes, the flies small, dark, weak, oval, with fairly characteristic venation ; (3) The Chrysogastrini by their straight face and projecting epistoma, flattened abdomen and pubescent spots upon the face and wing venation ; (4) The Sphegini with rather markedly produced epistoma, non-tuberculate face and petiolate abdomen ; (5) The Myioleptini which have the hind femora thickened and usually spinose and the face usually tuberculate in the males, always concave in the females ; (6) Cheilosini, in which the radial sector always has bristles and usually many, and the face is tuberculate in both sexes except *Ferdinandea* and *Brachyopa*. It is possible that *Brachyopa* and its subgenus *Hammerschmidtia* should either go into a tribe of their own or be combined with Myioleptini, in which case they would be generalized elements. *Cynorhinella* possibly should be assigned to the Myioleptini. *Pia* has been tentatively assigned to the Chrysogastrini because of its probable affinities with *Psilota*, and that genus has been placed in the Chrysogastrini because of its elongate antennae and projecting epistoma, its convex abdomen notwithstanding.

It is believed that the higher Cheilosinae have the tuberculate face, the tubercle therefore representing a specialization which is being assumed instead of being lost. In these tribes the tubercle is occasionally present, or present in males, and in another tribe, the Cheilosini, it is a characteristic possession.



The remote genera of this subfamily contain the phylogeronts *Rhingia*, *Alipumilio*. The subfamily contains six tribogenera; nine genera; nineteen subgenera, of which those of minor value are: *Heringia*, *Cnemodon*, *Triglyphus*, *Chilomyia*, *Endoiasimya*, *Orthoneura*, *Plesia*, *Liogaster*, *Hemilampra*, *Eumyiolepta*.

*A key to the groups of the Cheilosinae.*

1. Face below drawn out into a long straight porrect snout; third vein and costa drawn down far below wing apex (*Rhingini*) ..... *Rhingia* Scopoli.  
Without such snout; third vein and costa end at apex ..... 2
2. Face without tubercle; epistoma sometimes protuding ..... 3  
Face with a tubercle between epistoma and antennae, even though small; epistoma not sharply produced ..... 29
3. Wing with numerous radial sector bristles ..... 5  
Without radial sector bristles ..... 4
4. Face straight in profile, the eyes pilose, the epistoma never produced.  
Hind femora simple or rarely a little swollen distally; sometimes microdenticulate. Apical cross-vein never confluent with third vein at the apex of the wing (*Pipizini*) ..... 24  
Face either concave and produced diagonally forward upon lower half or face straight above with the epistoma projecting. Hind femora simple or if thick, it is very thick and denticulate ..... 7
5. Aeneous flies, with very strong bristles on thorax and scutellum; face barely concave on upper half, slightly rounded, but not tuberculate below ..... *Ferdinandea* Rondani.  
Not aeneous species; if with strong bristles the face is deeply concave and projecting obliquely below. Usually luteous in colour ..... 6
6. Thorax with strong, heavy microchaetae; abdomen more elongate ..... [Schummel]. *Hammerschmidtia*  
Thorax and abdomen only with strongly-developed pile; femora and tibiae more slender with less heavy spines ..... *Brachyopa* Meigen.
7. Face concave upon the upper half; projecting bluntly, obconically and diagonally forward upon the lower half; hind femora moderately thickened and usually spinose below. Antennae always short. Apical cross-vein usually confluent with third vein at wing tip; male face usually with a tubercle (*Myioleptini*). ..... 22  
Face upon upper half straight or slightly concave, but the epistoma always a little produced forward, sometimes considerably produced. Antennae short or long ..... 8
8. Abdomen elongate, slender, usually constricted at the base and often quite petiolate. Epistoma quite often considerably produced. Antennae always short (*Sphegini*) ..... 18  
Abdomen short, oval, compact or flattened. Antennae short or often quite elongate ..... 9
9. Abdomen compact, convex; eyes large, pilose; face quite concave.  
Hind femora massive, denticulate below ..... *Alipumilio* Shannon.  
Abdomen flattened, oval. Femora but little or not at all thickened (*Chrysogastrini*) ..... 10
10. Face straight and retreating to the epistoma which is produced a short distance. Antennae short or moderately lengthened. Abdomen convex and oval. Eyes densely pilose. Vena spuria absent ..... *Psilota* Meigen.

- Abdomen oval, usually wide, and much flattened. Eyes bare ;  
vena spuria usually present, though not always heavily developed. 11
- Head, thorax, abdomen, or all three, with flattened golden or silver  
scales ..... 12
- With only soft, normal pile ..... 13
12. Antennae short, the third segment wide and scarcely longer than wide. *Protolapidostola*, subg. n.
- Antennae elongate, sometimes longer than the face ; third segment  
many times longer than wide ..... *Lepidostola* Mik.
13. Apical cross-vein pulled out distally, or if the junction is nearly at  
right angles, the lower cross-vein is never parallel to the wing  
margin and the distance from the end of the lower cross-vein to  
the beginning of the apical cross-vein is quite short ..... 16
- Apical cross-vein joining the third vein definitely at right angles or  
even recurrent. The lower cross-vein is always oblique to the  
wing margin ; the distance from the end of the lower cross-vein  
to the beginning of the apical cross-vein is considerable ..... 14
14. Eyes dichoptic in males ; very shining species, usually large as  
compared to related groups ..... *Liogaster* Rondani.
- Eyes holoptic in males. Less metallic species ..... 15
15. Front without rugae. Hind femora without bristly spines. Third  
antennal segment very short. Vena spuria absent ..... *Hemilampra* Macquart.
- Front rugose. Hind femora with bristly spines. Third antennal  
segment elongate. Vena spuria faint ..... *Orthoneura* Macquart.
16. Eyesspotted or banded. Ocular pile, if present, uniformly distributed. 17
- Eyes unimaculate ..... *Chrysogaster* Meigen.
17. Eyes with small round spots ..... *Plesia* Macquart.
- Eyes with zig-zag or horizontal bands, particularly brilliant in life . *Chrysogaster* Meigen.
18. Abdomen strongly clubbed and petiolate. Third and fourth veins  
meet at a strong acute angle. Medium sized to large flies.
- Anterior wing border dark in known forms ..... 19
- Abdomen usually weakly club-shaped or petiolate. Third and  
fourth veins usually meet at right angles or nearly so ; never  
acutely and near wing tip. Small flies ..... 21
19. Face concave, never tuberculate. Males holoptic. Hind femora  
spinose beneath or pilose. Small cross-vein at the middle of the  
discal cell barely beyond or before, oblique ..... 20
- Face tuberculate, at least in the male, but possible non-tuberculate  
in female. Males dichoptic. Hind femora spinose beneath.
- Small cross-vein before the middle of the discal cell ..... *Valdivia* Shannon.
20. Hind femora with many strong short spines below ..... *Odyneromyia* Shannon.
- Hind femora with only soft pile below ..... *Takaomyia* H. B.
21. Wings with the outer backward angles of the subapical cell almost  
rectangular ; arista bare, about as long as the third segment.
- Third antennal segment elongate ..... *Neoascia* Williston.
- Wings with the lower angle of the subapical cell rounded. Arista  
usually pubescent, longer than the the third segment ; third  
segment rounded ..... *Sphegina* Meigen.
22. Front produced into a rather conspicuous antennal protuberance. *Chalcomyia* Williston.
- Eyes dichoptic in males ..... 23
- Front very little produced at the antennae. Males holoptic and  
tuberculate ..... *Eumyiolepta* Shannon.
23. Head, thorax or abdomen, or all three, clothed with flattened  
squamae ..... *Myiolepta* Newman.
- Body with only short pile, soft or setaceous .....



24. Antennae quite elongate. Eye pile arranged in zig-zag patches or at least with a bare, submedian, horizontal stripe. Face with patches of dense pubescence ..... *Trichopsomyia* Williston.  
 Antennae short, or only moderately elongate. Pile of eyes, when present, continuous. Face without dense areas of pubescence .. 25
25. Abdomen apparently composed of only three visible segments; fourth segment visible but small ..... *Triglyphus* Loew.  
 Abdomen with the usual number of well-developed segments ..... 26
26. Face much broader on the lower half than just below the antennae. *Pipiza* Fallen.  
 Lower part of face scarcely or not at all broader than the face immediately below the antennae ..... 27
27. The arista is bare microscopically; the eyes frequently have a horizontal bare stripe ..... *Pipizella* Rondani.  
 The arista is microscopically pilose to the apex; the eyes are always uniformly pilose ..... 28
28. The fourth abdominal sternite of the male is only about one-half as long as the corresponding tergite; female middle tibiae slender; female third antennal segment elongate; subcosta terminates past the anterior cross-vein ..... *Heringia* Rondani.  
 This sternite three-fourths as long as corresponding tergite; female middle tibiae rounded in front, or produced in the male; hind trochanters with a long process as a rule ..... *Cnemodon* Egger.
29. Abdomen elongate and petiolate or at least constricted at the base; eyes dichoptic; the facial tubercle small; males only (females non-tuberculate; see couplet 19)..... *Valdivia* Shannon.  
 Abdomen not elongate, and not constricted or petiolate ..... 30
30. Apical cross-vein meeting third vein at or almost at the extreme apex of the wing. In general all the femora more thickened and enlarged. Males only tuberculate (females non-tuberculate, see couplet 23) ..... 31  
 Apical cross-vein meeting third vein some distance back from the apex of wing. Femora usually more slender..... 32
31. Head, thorax or abdomen, or all three, clothed with squamulae... *Eumyiolepta* Shannon.  
 With only normal pile..... *Myiolepta* Newman.
32. Hind femora greatly thickened; lower face conically and diagonally produced forward and downward for a considerable distance, the facial tubercle subordinate ..... *Cynorkinella* Curran.  
 All the femora comparatively quite slender; face not produced ... 33
33. Eyes bare ..... 34  
 Eyes pilose ..... 35
34. Arita plumose ..... 36  
 Arita pubescent or bare ..... *Cartosyrphus* Bigot.
35. Arita long and loose plumose ..... *Hiatomyia* Shannon.  
 Arita densely and thick plumose, feather-like ..... *Taeniochilosia* Oldenberg.
36. Arita plumose ..... *Endoiasimyia* Bigot.  
 Arita pubescent or bare ..... *Cheilosia* Meigen.

## Tribe CHEILOSINI.

## CHEILOSIA Meigen.

*Cheilosia* Meigen, *Syst. Beschreibung*, 3, 296 (1822).

*Chilosia* Williston, *Bull. U.S. Nat. Mus.* 31, 38 (1866) and authors.

Small to medium sized and sometimes up to 15 mm. Almost without exception dark coloured, black, sepia, blue-black or aeneous flies and almost never with a

pattern upon the abdomen. Frequently long pilose or bristly flies. Head with face tuberculate in both sexes. Antennae short. Face short or often deeply produced downward, rarely forward. Facial stripes with or without pile. Humeri pilose. Scutellum often with marginal bristles, metasternum pilose. Abdomen oval. Wings with venation not unlike *Syrphus* except that the third vein is almost always greatly arched, not sinuous and the subapical cross-vein less sinuous. The costa ends at the apex of the wing. The first posterior cell is frequently more elongate in the males. The author does not view the downward extension of the frontal lunule, which in some species separates the antennal pits, as of generic significance. Genotype—*Syrphus flavipes* Panzer.

Distribution: palaearctic 164; nearctic 66; neotropical 10; oriental 59; Australian 7; holarctic none; fossil species 10.

*Cartosyrphus* Bigot (subgenus), *Ann. Ent. Soc. Fr.* (6), **3**, 230 (1883).

These are short pilose *Cheilosia*-like flies with bare eyes; apart from slight intangibles these are the only differences from *Cheilosia* and it seems that ocular pilosity is the basis for only a subgeneric distinction. Genotype—*Syrphus pagana* Meigen.

Distribution: palaearctic at least 49 (these included in the total *Cheilosia* for the palaearctic); nearctic 27; holarctic, possibly 1.

*Hiatomyia* Shannon (subgenus), *Insec. Inscit. Menstr.* **10**, 126 (1922).

These are small, short pilose species of *Cheilosia* with bare eyes and plumose arista. This is a very distinct group. The third antennal segment is equipped with one or more large pores often forming a seam. Subgenotype—*willistoni* Snow.

Distribution: nearctic 22.

*Endoiasimyia* Bigot (subgenus), *Ann. Ent. Soc. Fr.* (6) **2** and (6) **3**, 229 (1883).

*Sonanomyia* Shiraki, *Mem. Fac. Sci. Agric. Taihoku*, **1**, 320 (1930).

These are small, short pilose *Cheilosia* with plumose arista but pilose eyes. The author (1943) at one time regarded the group as equivalent to *Hiatomyia* which, however, has bare eyes. Subgenotype—*indianus* Bigot.

Distribution: palaearctic 2. Upper India 1, Japan 1.

*Eocheilosia*, new subgenus. This name is proposed for those species of *Cheilosia* with the male eyes widely dichoptic. Subgenotype—*Cheilosia ronana* Miller.

*Taeniochilosia* Oldenberg (subgenus), *Wien Ent. Ztg.* **35**, 101 (1916).

Small *Cheilosia*-like flies, the eyes bare; the arista is thickly and densely plumose to the apex, somewhat as in *Copestylum*. As, according to the figure, the arista arises apically, this form may belong to the Pelecoceratinae. Subgenotype—*atriseta* Oldenberg.

Distribution: palaearctic 1.

*Stenocheilosia* Matsumura (genotype *issiki* Mats.) is unknown to the author. *Cheilosia pedunculata* Bigot from Gabon may safely be expected to belong elsewhere.

Not recognized: *Chilomyia* Shannon, *Insec. Inscit. Menstr.* **10**, 127 (1922).



*Dasychilosia* Enderlein, for *variabilis* Panzer, is a synonym.

Based purely upon the presence of pile upon the sides of the face, this is regarded as a species group; at least 20 palaearctic species fall here; 14 are nearctic. Based upon *occidentalis* Williston.

Not recognized: *Portevinia* Goffe, *Ent. Mon. Mag.* **80**, 244 (1944). For *Eristalis maculatus* Fall. (*Cheilusia maculata* Fall.).

Not recognized; the alleged characters of the fly, which is before me, are not of generic value or significance.

*Chaetochilosia* Enderlein, *Die Tierwelt Mitteleuropas*, **6** (2), Ins. 3, 1-259. For *C. mutabilis* Fallen.

Based upon hairy-eyed, bare-faced species in which the scutellum has bristles. The presence of bristles upon the scutellum is not regarded as of generic significance.

#### NEPHOMYIA Matsumura.

It is not easy to decide upon the exact affinities of this fly (known from female only); Shiraki did not mention it; its author thought it related to *Nausigaster* but it is not even remotely similar. I have before me the description and the illustration (a dorsal view only) which were given of it. The venation might be that of *Cheilusia*; the abdomen described as oval must be very widely oval from the figure; its apex was said to be strongly curved downward, however, and it is a rather long pilose fly, the pile rather thick; scutellum simple; hind femora slender but a little longer and thicker than the others; eyes pilose. Marginal cell open, the third vein straight, the anterior cross-vein basal, the sixth vein straight, the first posterior cell with a well-developed apical stalk. Of the face, Matsumura said: "face black, beak-like produced, vertically, in the middle with a low tubercle, oral margin deeply excavated . . . antennae short . . . third segment nearly quadrate".

No comment was made of the presence or absence of pile upon the humeri or metasternum. This fly may be presumed to be a member of the Cheilosinae, but more data is also needed upon the appearance of the face in order to place it exactly. Genotype—*bombiformis* Matsumura.

*Spheginascia* Meunier (fossil genus). Characterized by: eyes holoptic; male face with a broad, convex, tuberculate bulge on lower face; female face concave with no bulge; hind femora slender, bristly spinose. Wings with both apical and postical cross-vein nearly oblique and confluent with the third and fourth veins remote from the wing margin. Genotype—*biappendiculata* Meunier.

#### FERDINANDEA Rondani.

*Ferdinandea* Rondani, *Nuova Ann. Sci. Nat. Bologna*, (2), 196 (1844).

These are medium sized, bright brassy or golden flies with strong bristles on the pleura, post-calli and scutellum; face much like *Syrphus* and slightly concave, with long, low, gradually rounded tubercle; face well developed but not produced. There are also well-developed facial stripes as in *Cheilusia* and numerous radial sector bristles. Antennae short; third segment short oval. Eyes pilose. There

are great, long macrochaetae upon the scutellum and notopleura, mesopleura, supraalae and the post-calli. The abdomen is elongate, oval and rather convex. Hind femora short but not thickened, and unarmed. Venation with sinuous third vein and subapical cross-vein; the latter ending not so close to the wing apex. Genotype—*Conops cuprea* Scopoli.

Distribution: palaearctic 4; nearctic 5; oriental 5.

*Ferdinandeia* has numerous features not unlike that of Volucellinae.

#### BRACHYOPA Meigen.

*Brachyopa* Meigen, *Syst. Beschreibung*, 3, 260 (1822).

Small or more seldom medium-sized flies, usually always of luteous, orange-brown, or light reddish coloration, but sometimes dark. The face is concave in both sexes, the lower part rather produced diagonally forward. Antennae short, the arista often long pubescent. Eyes bare; approximate in the male. Abdomen short and wide, not very convex. Hind femora simple. Venation somewhat *Cheilosia* or *Myiolepta*-like, the third vein nearly straight, the nearly straight subapical cross-vein meeting the third vein near the wing apex. Genotype—*Rhingia bicolor* Fabricius.

Distribution: palaearctic 7; nearctic 13; Australian 1.

Recognized subgenera: *Hammerschmidtia* Schummel, *Isis*, 7, 740 (1834).

Flies of reddish colour and face similiar to *Brachyopa*. Arista short plumose; head triangular from in front; eyes approximate in male; hind femora moderately thickened; thorax with moderately strong bristles. Venation similar to *Brachyopa*. Subgenotype—*Rhingia ferruginea* Fallen.

Distribution: palaearctic 3; nearctic 1; holarctic 1.

#### CYNORHINELLA Curran.

*Cynorhinella* Curran, *Canad. Ent.* 54, 14 (1922).

Medium-sized black flies with greatly produced face, the direction diagonally forward and downward. Face tuberculate in both sexes. Antennae short. The upper half of the face lacks facial stripes and crease. The front is only moderately prominent. Eyes holoptic from a short distance and bare. Abdomen of the *Cheilosia* type. Hind femora considerably thickened, with a large, lateral, ventral, distal flange or plate. Venation rather like *Myiolepta*; subapical cross-vein enters the third vein almost exactly at the tip of the wing; anterior cross-vein before the middle of the discal cell, but near it. Genotype—*canadensis* Curran.

Distribution: nearctic 2.

#### Pia Philippi.

*Pia* Philippi, *Verh. Zool.-bot. Ges. Wien*, 15, 742 (1865).

Small, blue-black flies with orange antennae, yellowish and pilose face, bare eyes and hyaline wings. Spurious vein absent. Femora slender, unarmed. The characters given are insufficient for a clear understanding of this fly, not taken, apparently, since it was originally described. It appears to belong to the Cheilosinae. The slender, unarmed femora would eliminate the possibility of its belonging



to the Myioleptini. It may be related to *Cheilusia* or *Pipiza*, and to the author it seems still more likely that it is related to *Psilota*. Genotype—*cyanea* Philippi.

Distribution : neotropical (Chile) 1.

#### Tribe PIPIZINI.

These are small, dark coloured flies characterized by the retreating face, which may be shallowly concave. Eyes pilose. Face black. Abdomen rarely marked with yellow.

#### PIPIZA Fallen.

*Pipiza* Fallen, *Nova Dipt. Disp. Method*, 2, 32 (1810).

This genus contains small, weak-flying species of dark coloration, occasionally with paired yellow spots. Face rather broader at the oral margin than at antennae. The antennae are short ; third segment never elongate and seldom twice as long as wide. Hind femora a little thickened, especially distally, and sometimes the ventro-apical region is equipped with two rows of short, subspinose bristles or spinose setae. Genotype—*Musca noctiluca* Linnaeus.

Distribution : palaearctic 15 ; nearctic 26 ; neotropical 7 ; oriental 1 ; holarctic 1 ; fossil species 2.

Recognized subgroups :

*Trichopsomyia* Williston (subgenus), *Trans. Ent. Soc. Amer.* 15, 259 (1888).

*Halictomyia* Shannon, *Proc. U.S. Nat. Mus.* 70, No. 9, p. 13 (1927). Based on *boliviensis* Shannon (identical).

Dark coloured *Pipiza*-like flies, the pile of eyes arranged more or less as patchy spots, or with bare stripes. Antennae set at middle of head and quite elongate, all segments participating ; face with area of dense pubescence along the eye margins. No scale-like pile. Vertex swollen. Face below antennae gently retreating, with a very small, low tubercle in the female. Abdomen elongate oval ; four segments in male, five in female visible ; abdomen flat on disc, thin on the sides. Hind femora somewhat thickened upon the distal half ; hind tibiae usually much swollen and thickened, its whole dorsal length with a strong brush of hair. Hind basitarsi short, much thickened. Apical cross-vein tends to be directed obliquely outward on last section, meeting third vein near wing apex. Genotype—*polita* Williston.

Distribution : neotropical 8.

*Pseudopipiza* Hull (fossil subgenus). Characterized by : face bulges out convexly on the lower half, but is non-tuberculate ; it is gently concave above ; apical cross-vein joins the third vein close to tip of wing. Subgenotype—*antiqua* Hull.

*Heryngia* Rondani (subgenus), *Dipt. Ital. Prodr.* 1, 53, 28 (1856).

These are *Pipiza*-like flies in which the face below is more narrow and is about as wide as the width at the antennae. The front is a trifle swollen. Antennae short in males, longer in females, their arista microscopically pubescent to the apex. Male fourth sternite only about half as long as the length of its tergum. The middle tibia is slender in both sexes. Pile of eyes evenly spread which, together with the slender middle femur, narrow face, helps to distinguish the females.

Kowartz gave these distinctions: convexity of the front in the male and absence of the white spots of the front in the female. These are trivial. Genotype—*Pipiza heringi* Zetterstett.

Distribution: palaearctic 7; nearctic 4.

*Cnemodon* Egger (subgenus), *Verh. Zool.-bot. Ges. Wien*, **15**, 573 (1865).

These *Pipiza*-like flies have the face comparatively narrow below, the antennae short, their arista microscopically pubescent to the apex. Fourth sternite three-fourths as long as its tergite; middle tibiae of male produced in front; the hind trochanters in male usually with a long process. Subgenotype—*latitarsis* Egger.

Distribution: palaearctic 4 (probably more); nearctic 24.

*Pipizella* Rondani (subgenus), *Dipt. Ital. Prodr.* **1**, 54 (1856).

In this group the face is narrow below. Antennae elongate, more than twice as long as wide; generally with a length three or more times the width; arista microscopically bare, rarely pilose at immediate base. The eyes in both sexes show a median horizontal stripe that is bare. The last section of the fourth vein is somewhat angulated or bent near its middle. The elongate antennae, apilose ocular stripes lead to *Trichopsomyia*. Subgenotype—*Mulio virens* Fabricius.

Distribution: palaearctic 4; nearctic 10; oriental 3.

*Triglyphus* Loew (subgenus), *Progr. Posen*, **15**, 30 (1840).

*Pipiza*-like flies in which the abdomen is usually said to be composed of only three visible segments; actually, however, the fourth segment is visible but small. The face is quite short, virtually straight, and retreating. Subgenotype—*primus* Loew.

Distribution: palaearctic 2; nearctic 2; oriental 1; Australian 1.

*Emmyia* Klocker (subgenus), *Mem. Queensland Mus.* **8**, 55 (1924).

A *Pipiza*-like fly in which the epistomal region is a little produced. The eyes are holoptic and densely hairy. The vena spuria is distinct. Related to *Psilota* on the one hand, to *Pipiza* on the other. A few particulars are quoted from Klocker: "front not protruding; epistoma only a little protruding. Face not hollowed out below antennae and without central tubercle. Anterior cross-vein very close to base of discal cell. A densely pilose fly". Subgenotype—*queenslandica* Klocker.

Distribution: Australian 1.

*Stenopipiza* Matsumura (genotype—*bipuncta* Matsumura) is unknown to the author.

Not recognized: *Penium* Philippi, *Verh. Zool.-bot. Ges. Wien*, **15**, 741 (1865). From Chile. Apparently identical with *Pipiza*. Based on *triste* Philippi.

### Tribe CHRYSOGASTRINI.

#### CHRYSOGASTER Meigen.

*Chrysogaster* Meigen, *Nouvelle Classification*, 32–61 (1800).

Small flies, always dark in colour and usually metallic. Face with epistoma produced and concave or in the males of a few species with small inconspicuous



tubercle. Face with a rugulose patch, better called striate. Eyes bare, often with zig-zag pattern. Front, especially in female, with rugae. Abdomen short, oval, flattened. Scutellum with the edge tending towards a differentiated margin. Genotype—*Eristalis solstitialis* Fallen.

Distribution : palaearctic 40 ; nearctic 23 ; neotropical 7 ; Ethiopian 9 ; oriental 5 ; Australian 5 ; fossil species 1.

Recognized subgenera : *Liogaster* Rondani, *Dipt. Ital. Prodr.* 2, 166 (1857).

These are *Chrysogaster*-like, small, metallic flies in which the males are dichoptic. Subgenotype—*Chrysogaster splendida* Meigen.

Distribution : palaearctic : found there, the number undetermined ; nearctic found there, the number also undetermined.

*Plesia* Macquart (subgenus), *Dipt. Exot. Suppl.* 4, 152 (1849).

*Chrysogaster*-like flies with the eyes spotted, bare and broadly touching ; upper facets much enlarged. Antennae short. Face concave with well-developed tubercle and thence concave to the produced epistoma. Lower cross-vein strongly recurrent and straight ; apical cross-vein nearly straight but parallels the wing margin and enters the third vein remote from the apex of the wing. Vena spuria practically absent. Genotype—*anale* Macquart.

Distribution : Australian 1.

*Orthoneura* Macquart (subgenus), *Rec. Soc. Sci. Agric. Lille*, 188 (1828).

Eyes are narrowly touching in the male ; front long, flat, in the male without rugae. Third antennal segment quite elongate. Hind femora without bristly spines. Vena spuria faint. Subapical cross-vein recurrent or nearly rectangular, usually straight ; postical cross-vein nearly straight, strongly directed away from the wing margin. Subgenotype—*Chrysogaster elegans* Meigen.

Distribution : palaearctic present ; nearctic present ; numbers undetermined.

Not recognized : *Liochrysogaster* Stackelberg, *Wien Ent. Ztg.* 41, 1-3 (1924), based on *przewalskii* Stackelberg, from Chinese Turkestan. He called it intermediate between *Liogaster* and *Orthoneura*. Also *Barberiella* Shannon, *Ins. Inscit. Menstr.* 10, 122 (1922), based on *chilosoides* Shannon, from California, a *Chrysogaster* with a *Cheilosia*-like facies.

*Hemilampra* Macquart, *Dipt. Exot. Suppl.* 4, 159 (1849).

Face very short above, considerably produced forward upon the lower two-thirds, the produced part bearing above a large conspicuous, obtusely rounded tubercle. Antennae quite short, the third segment perhaps shorter than deep, and sub-orbicular. Eyes bare, unmarked and long holoptic. Sides of face with faint subvertical striations. Metasternum bare or pubescent ; scutellum with impressed rim, without fringe. Abdomen flattened, short oval, wider than the thorax. Hind femora stout but not thickened, with only soft pile beneath ; hind basitarsi enlarged. Apical and lower marginal cross-veins straight, the latter very recessive and ending in the fourth vein much farther from the apical cross-vein than its own length. Third vein perfectly straight ; petiole of the first posterior cell a little longer than the apical cross-vein ; vena spuria quite absent. Genotype—*australis* Macquart.

Distribution : Australian 1.

## ALIPUMILIO Shannon.

*Alipumilio* Shannon, *Proc. U.S. Nat. Mus.* **70**, No. 9, p. 12 (1927).

A phylogeront. Remarkable flies with very thick, short, stubby or bristly pilose eyes, reduced face, produced epistoma, concave face jutting below into a kind of beak, massive hind femora and characteristic venation. More details have been secured from the type as follows: face quite narrow, from the front almost parallel, more narrow below; occiput much reduced. First antennal segment short; third rather large, nearly twice as long as wide; arista short, micropubescent. Thorax rather convex, very broad, amazingly punctate, quite short; scutellum long, broad, with impressed rim and no fringe. Squamae large, bare with long fringe. Abdomen with five visible segments; short and broad and reflexed downward at the third segment; pile stubby and golden, on the last segment vorticular, the whole surface grossly punctate. Hind femora massive, multi-microdentate; tibiae strongly arcuate, with serrate knife-edge, apex nearly plane. The straight third vein ends at apex of wing; the apical cross-vein is quite recurrent and almost straight; small cross-vein enters fourth vein two-fifths from base of discal cell. Genotype—*femoratus* Shannon.

Distribution: neotropical (Amazon) 1.

## LEPIDOSTOLA Mik.

*Lepidostola* Mik, *Wien Ent. Ztg.* **5**, 278 (1886).

Odd, peculiar, small flies of dark colour, beset with silver or golden scales and scale-like hair. Antennae quite elongate. Face short, retreating with a small, inconspicuous tubercle, sometimes two. Face with characteristic patches and streaks of dense pubescence as in *Chrysogaster*, *Trichopsomyia* but no true stripes above the cheeks. Abdomen short oval. Hind femora considerably thickened and ornamented with a double row of heavy spines. Other femora also spinose. Wing venation fairly characteristic. Apical cross-vein long, meeting third vein at apex of wing, sometimes strongly angulated, with or without spur. Anterior cross-vein basal. Rare flies. Genotype—*calopus* Loew.

Distribution: neotropical 14.

*Protolepidostola* Hull (new subgenus), for *scintillans* Hull.

Distinguished from *Lepidostola* only by the quite short, oval, third antennal segment in contrast to the extremely elongate antennae characteristic of *Lepidostola*.

## PSILOTA Meigen.\*

*Psilota* Meigen, *Syst. Beschreibung*, **3**, 256 (1822).

These are small flies, entirely dark or metallic in colour with fairly large antennae and with concave face in both sexes, the epistoma produced. Eyes thick pilose. Abdomen subglobose. Genotype—*anthracina* Meigen.

Distribution: palaearctic 5; nearctic 3; oriental 4; Australian 11.

\* *Parapsilota*, new subgenus, has been erected by Hardy with *viridis* Macquart as subgenotype. *Proc. Roy. Soc. of Queensl.* vol. xlv. p. 16 (1933). A valid subgenus including several species. Hardy remarks that both subgenera break up into several species-group.



## COELOPROSOPA Macquart.

*Coeloprosopa* Macquart, *Dipt. Exot. Suppl.* 4, 145 (1849).

Face concave, without prominence; epistoma projecting. The front in the female projects somewhat also. First two segments of antennae short; third oval, convex on the upper part, almost straight beneath; arista basal; bare. Eyes short pilose. Scutellum bordered. The abdomen is narrowed posteriorly, the female terminal ovipositorial segments elongate. The posterior femora are swollen with a ventral, subapical tooth, and spinose and pilose beneath; hind tibiae a little swollen and arched. Wings with the external medial vein straight; first transverse vein situated at a sixth from the discoidal cell (translation). Genotype—*nitida* Macquart.

Distribution: Australian (Tasmania) 1.

Macquart thought his genus related to *Xylota* and to *Eumerus*. Major E. E. Austen left notes at the British Museum stating that the type had the appearance of a *Psilota* with elongate abdomen; this is not improbable, the locality considered, as well as its broadly open submarginal cell. The type was not found at the British Museum.

## Tribe SPHEGINI.

Characterized by the slender form and concave face with the epistoma usually rather strongly produced. The abdomen is usually petiolate, sometimes quite petiolate.

## SPHEGINA Meigen.

*Sphegina* Meigen, *Syst. Beschreibung*, 3, 193 (1822).

Small, slender flies, the abdomen at least a little narrowed basally, but usually quite slender, the apex club-like in both sexes. Hypopygium large. The epistoma is strongly produced, the face concave. Antennae short; eyes dichoptic in male. Hind femora somewhat thickened with a row of spines below. Face brownish or often yellowish. Abdomen usually marked with pairs of spots. Wings with the two marginal cross-veins ending far from the wing margin, their basal spurs usually absent. Genotype—*Milesia clunipes* Fallen.

Distribution: palaearctic 13; nearctic 25; neotropical 1 (probably belongs elsewhere); oriental 10; fossil species 2.

## SPHEGINOIDES Szilady.

*Spheginoides* Szilady, *Ann. Hist. Nat. Mus. Hung.* 32, 138 (1939). For *obscura* Szilady, from Europe. Not seen by author.

*Pseudosphegina* Hull (fossil genus). Characterized by: venation like *Sphegina*; face tuberculate; males narrowly dichoptic. Genotype—*dichoptica* Hull.

*Palaeascia* Meunier (fossil genus). Characterized by: eyes holoptic; face tuberculate; hind femora but little thickened and with a double row of spines; apical and postical cross-veins both straight and join their respective veins remote from the margin of the wing. Genotype—*uniappendiculata* Meunier.

*Palaeosphegina* Meunier (fossil genus). Characterized by: venation like *Sphegina*; vena spuria absent. Males macroholoptic. Face tuberculate. Genotype—*elegantula* Meunier.

Not recognized: *Desmetrum* Enderlein (for *macrum* Enderlein), *S.B. Ges. naturf. Fr. Berl.* 193 (1937). I am unable to discover in the characterization of its author any characters which adequately separate this fly from *Sphegina*. The unusually basal anterior cross-vein and the type locality suggest that it may be *Chamaeosphegina* Shannon and Aubertin.

#### NEOASCIA Williston.

*Neoscia* Williston, *Bull. U.S. Nat. Mus.* **31**, 111 (1886).

Quite small, metallic flies, the abdomen petiolate, but less so than in *Sphegina* and the hypopygium smaller. Face produced downwards as well as forwards; only a little concave; eyes dichoptic in male. The antennae are more elongate than in *Sphegina*. Abdomen sometimes with pairs of small yellowish spots. Hind femora enlarged; spinose below. Wings with the two marginal cross-veins ending far from the end of the third and fourth veins, nearly straight, and ending nearly at a right angle. Genotype—*Syrphus podagricus* Fabricius.

Distribution: palaearctic 9; nearctic 9; oriental 1.

#### TAKAOMYIA Hervé-Bazin.

*Takaomyia* Hervé-Bazin, *Ann. Ent. Soc. Fr.* **83**, 412 (1914).

These are unique, strongly petiolate, somewhat wasp-like flies with produced front and concave face. The eyes are large and bare, and narrowly dichoptic in the males, their upper facets enlarged. Front a little produced, without pile. Antennae large; third segment a little longer than wide. Occiput cut away behind vertex, creased, and below thickened, much as in *Brachyopa*. Thorax elongate; humeri pilose; mesonotum pollinose vittate; metasternum pubescent only. Abdomen elongate-petiolate, subcylindrical, the second segment is narrowest; terminal portion with rounded club-like hypopygium. Hind femora elongate, a little thickened through middle, with only soft pile beneath. Subapical cross-vein joins third vein near apex; marginal cell open. Anterior cross-vein straight, oblique, but slightly beyond the middle (distalward) of the discal cell. Genotype—*johannis* Hervé-Bazin.

Distribution: palaearctic (Formosa) 2.

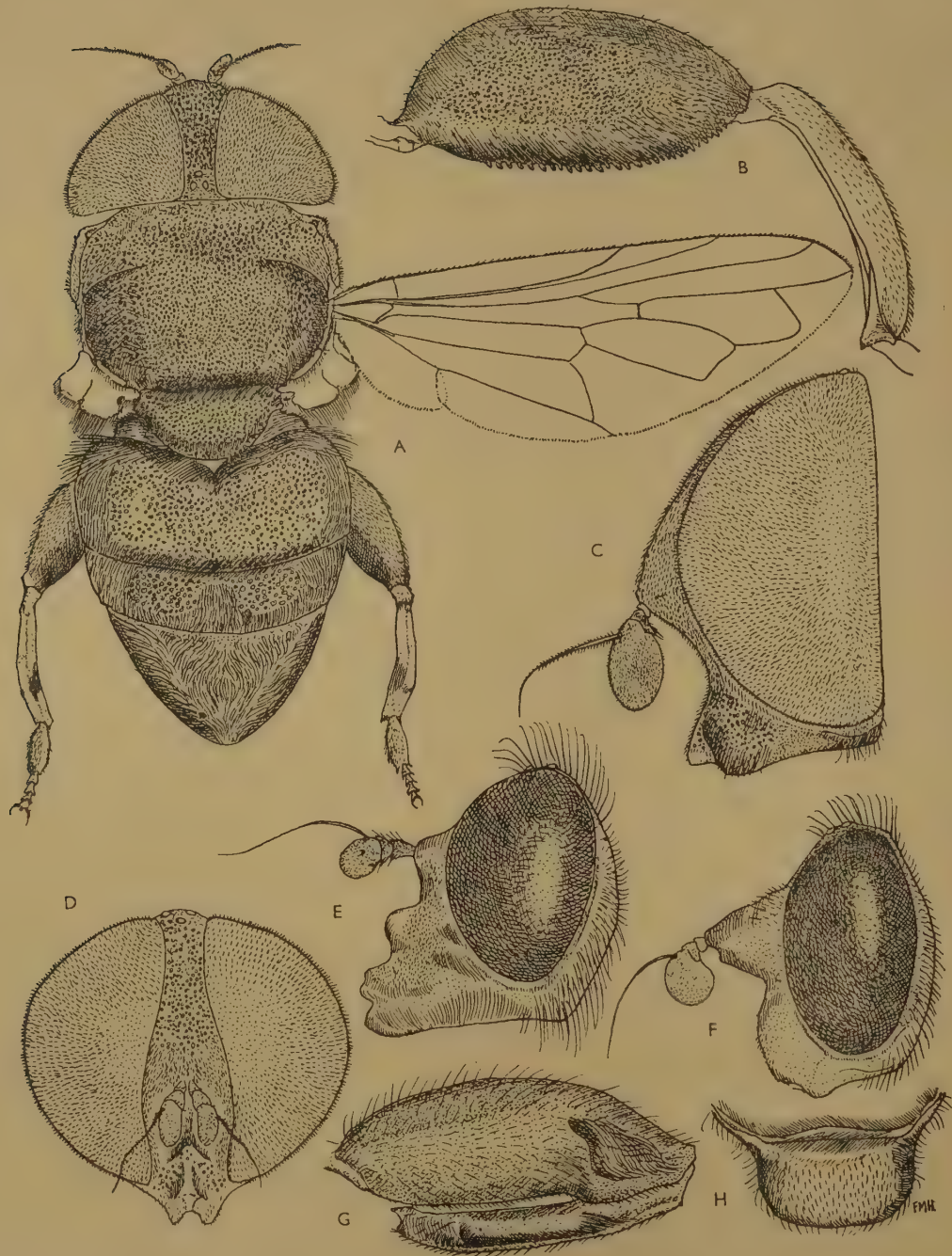
#### ODYNEROMYIA Shannon and Aubertin.

*Odyneromyia* Shannon and Aubertin, *Dipt. Patagonia, S. Chile*, **6**, 156 (1933).

Wasp-like medium-sized flies of blackish aspect, often relieved by light coloured antennae, legs or wings. Face markedly concave but with a small tubercle below the eyes. Eyes in male touching; upper facets slightly enlarged; vertical triangle tuberculate. Front strongly produced. Antennae short; third segment wider than long; arista long, thickened basally, bare. Front and face on the sides without pile. Thorax elongate, convex; humeri pilose. Abdomen subcylindrical



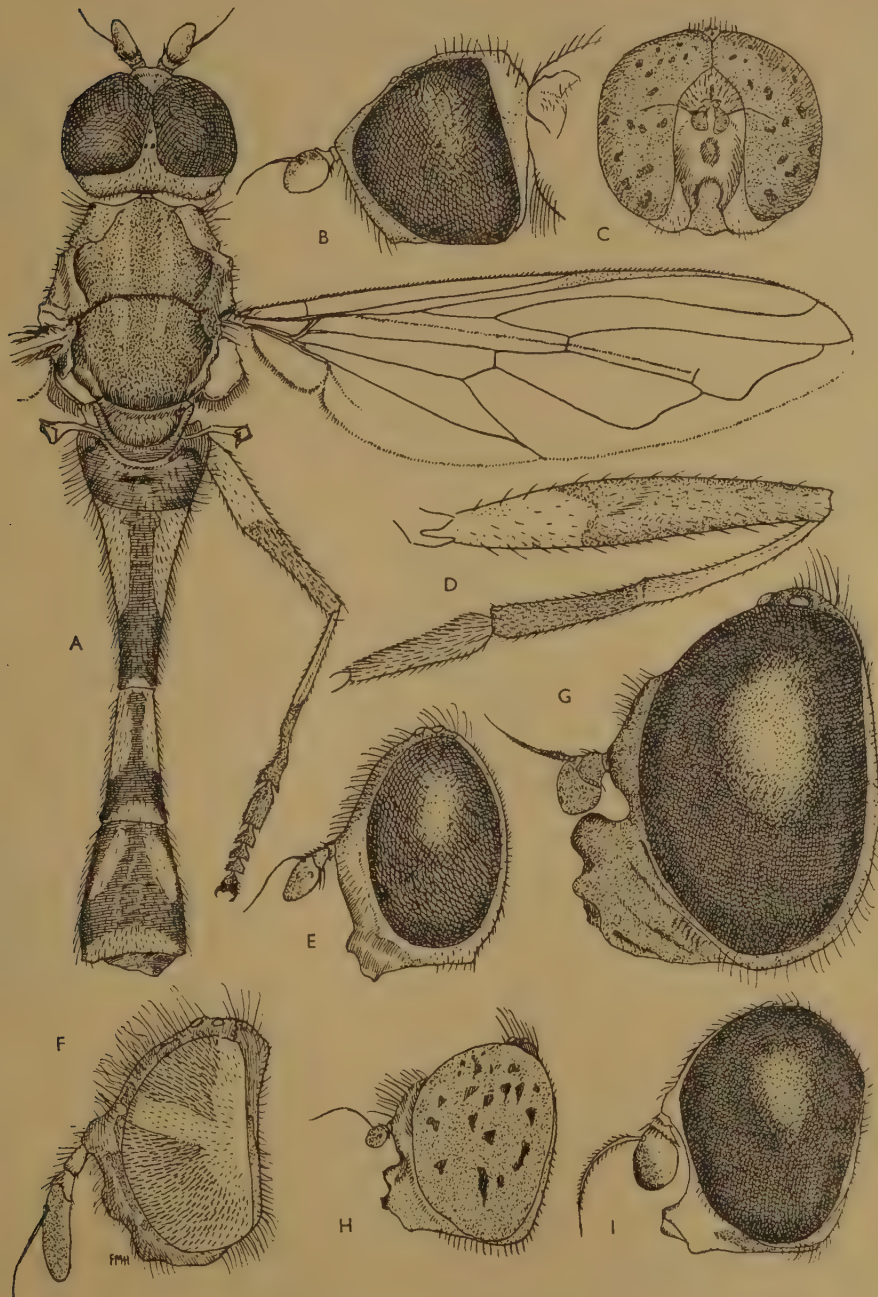
Fig. 16.



## The Subfamily Cheilosinae.

- A. *Alipumilio femoratus* Shannon, dorsal view (type); B. *Alipumilio femoratus* Shannon, hind femur and tibia (type); C. *Alipumilio femoratus* Shannon, profile of head (type); D. *Alipumilio femoratus* Shannon, front of head (type); E. *Cynorhinella bella* Williston, profile of head; F. *Cynorhinella bella* Williston, hind femur and tibia; G. *Chalcomyia aerea* Loew, profile of head; H. *Chalcomyia aerea* Loew, scutellum.

Fig. 17.



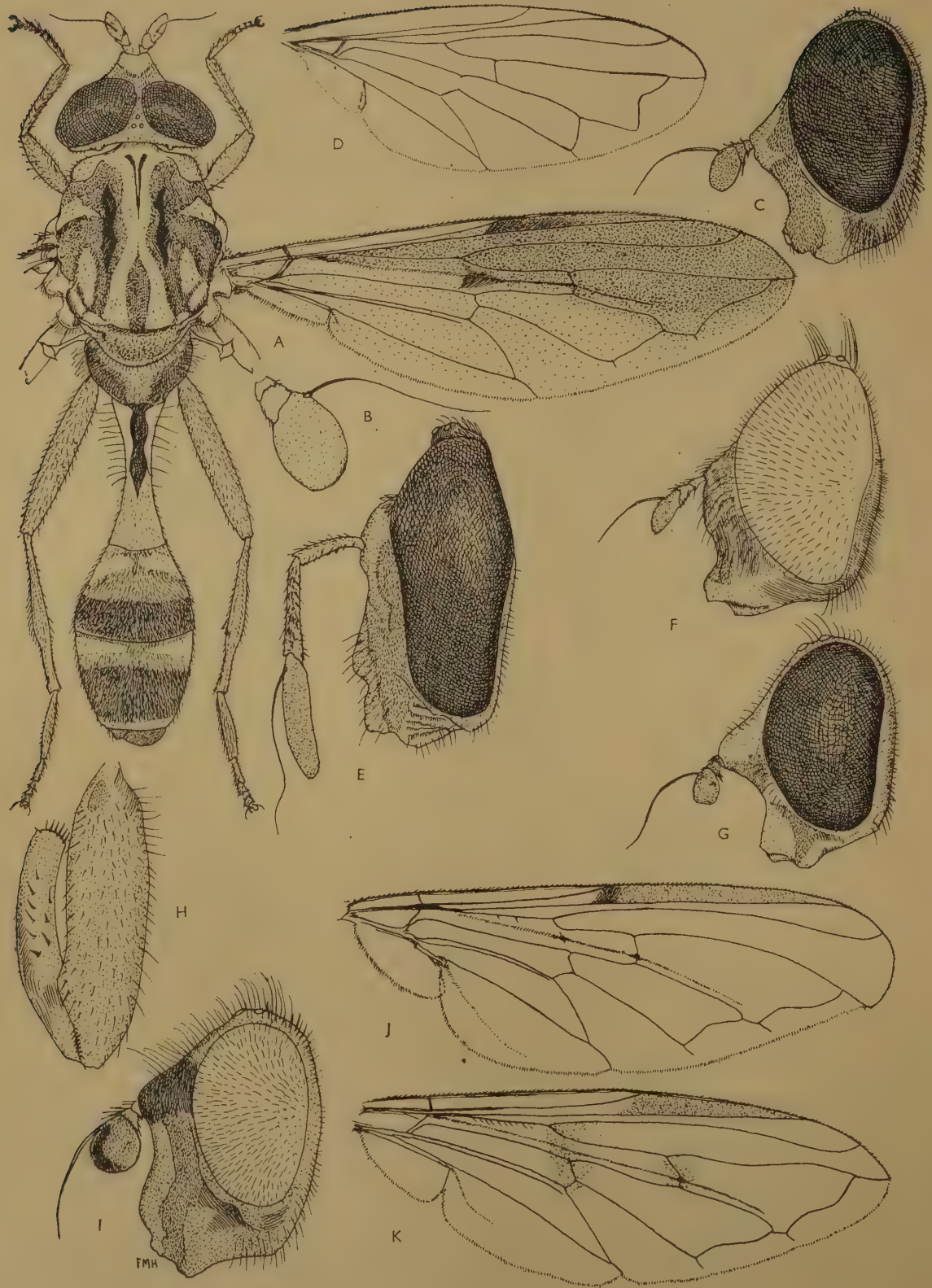
## The Subfamily Cheilosinae.

A. *Spheginobaccha* sp., dorsal view ; B. *Spheginobaccha* sp., profile of head ; C. *Plesia analis* Macquart, front of head ; D. *Spheginobaccha* sp., hind femur and tibia ; E. *Orthoneura nobilis* Macquart, profile of head ; F. *Trichopsomyia boliviensis* Shannon, profile of head ; G. *Hemilampra australis* Macquart, profile of head ; H. *Plesia analis* Macquart, profile of head ; I. *Sphegina flavimana* Malloch, profile of head.

and elongate and petiolate ; third segment widest and four or five times longer than broad. Hind femora elongate, a little thickened past the middle, spinose ventrally on both sides. Wings elongate ; apical cross-vein bent basally, drawn



Fig. 18.



out to apex of wing on its last part; third vein ends at apex; anterior cross-vein straight, oblique, and just before the middle of the discal cell; anterior wing margin brown. Genotype—*Doros odyneroides* Philippi.

Distribution: neotropical (Chile) 2.

#### VALDIVIA Shannon.

*Valdivia* Shannon, *Proc. U.S. Nat. Mus.* **70**, No. 9, p. 31 (1927).

Medium-sized flies of mostly dark colour, the legs frequently bright orange. Face of females concave, of males with at least a small tubercle; face without pile in both sexes. Eyes bare, dichoptic in the male. Palpi unusually long and slender. Metasternum bare. Abdomen elongate, gradually narrowed and constricted toward the base to a slight extent. Anterior cross-vein before the middle of the discal cell. Subapical cross-vein quite sinuous, with two angles. Alula as wide as second basal cell. Genotype—*darwini* Shannon.

Distribution: neotropical (Chile) 5.

#### CHAMAESPHEGINA Shannon and Aubertin.

*Chamaesphegina* Shannon and Aubertin, *Dipt. Patagonia, S. Chile*, **6**, 14 (1933).

Small, *Sphegina*-like flies, the femora simple and the venation somewhat different. Face short, concave, the epistoma projecting bluntly forward below. Antennae short, third segment barely longer than wide and subcircular. The abdomen is elongate, narrow, approximately parallel-sided, but in this respect not greatly different from certain nearctic species of *Sphegina*. Hind femora simple. Venation and wing shape slightly suggestive of *Sphegina*: anterior cross-vein very close to the base of the discal cell. However, in *Sphegina* that section of the discal cell length lying proximal to the cross-vein is little more than twice that of this fly. The apical cross-vein is oblique, nearly straight, long, and meets the third vein quite close to the apex of the wing; distance between postical and apical cross-veins greater than the length of the former. Genotype—*argentifacies* Shannon and Aubertin.

Distribution: neotropical (Chile) 1. Male unknown. It remains to be seen if the male is dichoptic as in *Sphegina*.

#### Tribe MYIOLEPTINI.

##### MYIOLEPTA Newman.

*Myiolepta* Newman, *Ent. Mag.* **5**, 373 (1838).

Small flies of dark colour, often metallic. Face concave in the females, the lower face slightly projecting diagonally; face of males tuberculate. Antennae short.

##### The Subfamily Cheilosinae.

- A. *Takaomyia johannis* Hervé-Bazin, dorsal view; B. *Takaomyia johannis* Hervé-Bazin, antenna; C. *Takaomyia johannis* Hervé-Bazin, profile of head; D. *Trichopsomyia boliviensis* Shannon, wing (type); E. *Lepidostola trilineata* Hull, profile of head (holotype); F. *Psilota buccata* Macquart, profile of head; G. *Myiolepta luteola* Gmelin, profile of head; H. *Hammerschmidtia ferruginæ* Fallen, hind femur and tibia; I. *Ferdinandea cuprea* Scopoli, profile of head; J. *Rhingia nigra* Macquart, wing; K. *Ferdinandea cuprea* Scopoli, wing.



Abdomen short oval. Hind femora only moderately thickened but with a prominent row or two rows of short spines ventrally. Venation *Cheilosia*-like except that the long, rather straight apical cross-vein meets third vein quite close to the apex of the wing. Genotype—*Musca luteola* Gmelin.

Distribution: palaearctic 7; nearctic 6; neotropical 4; oriental 1; fossil species 5.

*Eumyiolepta* Shannon (subgenus), *Bull. Brooklyn Ent. Soc.* **16**, 71 (1921).

Similar to *Myiolepta* in every respect except that much of the pile, especially upon the abdomen, is scale-like. Genotype—*Myiolepta strigilata* Loew.

Distribution: nearctic 3; neotropical 3.

Not recognized: *Sarolepta* Hull (based on *dolorosa* Hull) from Venezuela. A very aberrant type, but I am at present inclined to regard it as too close to *Myiolepta* for separation. It differs however in the very thin, non-rolled edges of the abdomen.

*Sericolepta* Hull (fossil subgenus). Characterized by: apical cross-vein joins third vein quite some distance from the tip of wing. Scutellum round-edged and convex (not with flattened, impressed rim). Spines of hind femora numerous. Subgenotype—*maculata* Hull.

*Arctolepta* Hull (fossil subgenus). Characterized by: non-tuberculate face; scutellum with chaetae; first posterior cell with a long distal stalk; hind femora stout with many bristly spines. Subgenotype—*calamitans* Hull.

*Cheilosialepta* Hull (fossil genus). Characterized by: venation of *Myiolepta*, but face non-tuberculate in both sexes; spines absent on hind femora; macrochaetae present on thorax. Genotype—*baltica* Hull.

#### CHALCOMYIA Williston.

*Chalcomyia* Williston, *Bull. Brooklyn Ent. Soc.* **12**, 133 (1885).

Head triangular from front. *Myiolepta*-like flies of dark or aeneous colour in which the males are widely dichoptic and the front quite produced. Antennae short, the third segment suborbicular, quite concave. Neither sex with a tubercle. Males with four abdominal segments. Genotype—*Myiolepta aerea* Loew.

Distribution: palaearctic 1; nearctic 6.

Not recognized: *Chalcosyrphus* Curran, *Kans. Univ. Sci. Bull.* **15**, 122 (1924). The only differences shown by the flies of this species group is a somewhat more thickened hind femora (in *Chalcomyia* already thickened), a flattened scutellum and thorax, and minor differences in the shape of the second antennal segment. Based on *atra* Curran (Missouri).

#### Tribe RHINGINI.

##### RHINGIA Scopoli.

*Rhingia* Scopoli, *Ent. Carniol.* 358 (1763).

A phylogeront. Medium-sized to small species at once distinguished by the long, porrect epistomal snout, thrust almost straight forward, far beyond the front.

Antennae short. Abdomen short, wide, rather convex. Coloration black to reddish brown, or cyaneous, rarely with brownish orange spots upon the abdomen. Wings with *Cheilosia*-like venation except that the costa and end of third vein are characteristically drawn far down below the apex of the wing. Genotype—*Conops rostrata* Linnaeus.

Distribution : palaearctic 6 ; nearctic 1 ; neotropical 3 ; Ethiopian 15 ; oriental 21 ; fossil species 1.

*Eorhingia*, new subgenus. This name is proposed for those species of *Rhingia* in which the male eyes are dichoptic. Subgenotype—*Rhingia cuthbertsoni* Curran.

*Protorhingia* Hull (fossil genus). Characterized by : the wing of *Rhingia* ; face concave, the epistoma but little produced. Genotype—*carpenteri* Hull.

*Cacogaster* Hull (fossil genus). Characterized by : marginal cell open ; third vein straight ; anterior cross-vein well before the middle of the discal cell ; spurious vein extensive ; costa and third vein end at tip of wing ; the abdomen is short and wide and was probably rather convex. Genotype—*novamaculata* Hull.

*Archalia* Hull (fossil genus). Characterized by : hind femora quite massive ; the anterior cross-vein lies well before the middle of the discal cell ; apical cross-vein quite sigmoid, joining the third vein well back from apex of wing ; third vein and costa end at apex. Genotype—*femorata* Hull.

#### THE SUBFAMILY CALLICERATINAE.

These are unique, handsome, metallic flies of medium size, at once distinguished by the elongate antennae and long slender terminal style rather similar to that of *Ceriodes*. They have occasionally been placed in the Cheilosinae, and they probably are most closely related to this subfamily. But to be consistent the styliform antennae must be weighed at the same evaluation here as in the subfamily Cerioidinae to which it gives character. Only the one genus is known.

#### CALLICERA Panzer.

*Callicera* Panzer, *Fauna Germanica*, 104, 17 (1806).

A remote genus. From the front the head is broadly oval. The eyes are densely pilose, with one or more bands of pile. The males are holoptic. The ocelli are set on a tubercle a little above the eyes. The front is short and prominent. The antennae are placed at the bottom of the upper fourth of the head in profile ; they are very elongate, and all the segments partake of the elongation ; the third segment ends in a style half as long as itself, in which three styler segments can be made out. The third styler segment is a little thicker than the first two, especially on the basal half, then tapers rapidly. The style is often snow-white. The antennae are held erect. The face below the antennae is very shallowly concave and retreats down to a low obtuse tubercle, the high point of which is just opposite the bottom of the eyes ; from there it quickly retreats so that the face is bluntly produced. The front is bare in the genotype. Face quite hairy. Occiput conspicuous in profile,



except near the top, thickly pilose. The thorax is elongate, rather convex, long thick pilose, the humeri equally pilose. The hemispherical convex scutellum has quite long thick hair. The abdomen is not quite twice as long as wide. It is widest at the end of the second segment where it is considerably wider than the thorax, thence tapers quickly to a point. The whole abdomen covered with long plush-like, very erect pile. On the legs the hind femora is scarcely thickened; ventroapically it possesses a few strong bristles on the outside, but it is not spinose. Wings with *Syrphus*-like venation, the apical and lower cross-veins at first shaped alike, at first they are bent inward slightly, then proceeding straight to their respective veins, the former joining the third vein only a short distance from the tip, at an acute angle. The third vein and costa end at the tip of the wing. The marginal cell is broadly opened, the third longitudinal vein practically straight but is a little curved down at the tip. The small cross-vein is oblique and located practically at the middle of the discal cell; vena spuria present. There is no stigmal cross-vein; the wings are a little pointed. The alula is well developed. The thorax and abdomen and the face of these flies are metallic and the abdomen particularly brilliant; in some species there are opaque markings. Genotype—*Syrphus aenea* Fabricius.

Distribution: palaearctic 9; nearctic 3; neotropical 1; oriental (Malay) 4.

#### THE SUBFAMILY PELECOCERATINAE.

This subfamily contains a few genera of small but characteristic flies with slender, non-petiolate abdomen. While only three genera are known, they show rather well an orthogenetic trend. The face is always variously produced forward and downward, except in *Chamaeosyrphus*, where it is merely rounded and bulging upon the lower half. The principal characteristics of the subfamily lies in the form of the antennae. The first two segments are quite short; the third is unusually large, nearly as deep as long, rounded and lobe-like ventrally and drawn out dorso-apically; a short distance from the apex of this segment the short, three-segmented, usually tumid arista emerges. Thus the third segment is subtriangular, for though round below, it is usually flat on top. In *Chamaeosyrphus* the arista is not greatly unlike that of a *Cheilosia* and is emitted in a forward direction from the antero-dorsal corner of the rounded third segment.

The species of *Pelecocera* to some extent intergrade with the curious *Ischyroptera*. Excepting the genotype, they have the same tumid cheeks and ventral occiput. The over-development of the cheeks and occiput might be a result of reduction in the size of the eye. In *Ischyroptera* the small cross-vein is right at the middle of the discal cell, while in all the others it is well formed and basal. Out of this we arrive at possibly a confirmation of the idea that the Syrphid wing as developed and specialized by having the anterior cross-vein move down the wing, gradually approaching the end of the discal cell, independently in more than one subfamily.

The flies of the subfamily have the legs simple and slender and unarmed. The humeri are pilose, the scutellum sometimes with apical bristles and without ventral fringe. The front of the head is narrow and polished. The occiput is often tumid and over-developed.

*A key of the groups of the subfamily Pelecoceratinae.*

1. Arista replaced by a curious, thickened, terminal style. Third antennal segment rounded and pendulous below and drawn out apicodorsally, until the segment is subtriangular ..... 2  
Arista thick, but otherwise normal; placed in about the middle of the upper border of the third segment. Anterior cross-vein before the middle of the discal cell. Third antennal segment more or less orbicular ..... *Chamaesyrrhus* Mik.
2. Anterior cross-vein placed at the middle of the discal cell; lower occiput and cheeks enormously developed. Face not smooth in contour ..... *Ischyroptera* Pokorný.  
Anterior cross-vein clearly lying before the middle of the discal cell. Lower occiput not extraordinarily developed. Cheeks usually not tumid or strongly developed ..... *Pelecocera* Meigen.

## CHAMAESYRRHUS Mik.

*Chamaesyrrhus* Mik, *Wien Ent. Ztg.* **14**, 133 (1895).

The head is broad and short, the occiput concave, when viewed from above, and with prominent flanges in the middle of the occiput. The vertex is almost exactly one-fourth of the head width (female). The antennae are separated; the first two segments small; the third thick, as well as large, and suborbicular. The basally strongly thickened arista is pointed straight outward, its tip acute, its body lying along the top of the segment. The face projects almost as much forward as downward. It is subtuberculate and pubescent. The facial stripes are well developed, below the cheeks and lower occiput very meagre. Thorax but slightly convex anteriorly, but posteriorly giving evidence of that pinched-in greatly convex, declivitous apex found so strikingly in *Chamaesphegina*. The calli and scutellum have long bristles; no ventral scutellar fringe; metanotum creased; humeri pilose. Abdomen slender, flat, margins curled, spotted and appressed setaceous. Metasternum bare. The wings are elongate; anterior cross-vein basal before the middle of the discal cell. The costa ends beyond the tip of wing. The subapical cross-vein a little longer than the lower marginal cross-vein. Subapical cross-vein joining third vein well back from the apex of the wing. Genotype—*Rhingia scaevoides* Fallen.

Distribution: palaearctic (Europe, Canary Is.) 9; nearctic 2; oriental (Java) 1.

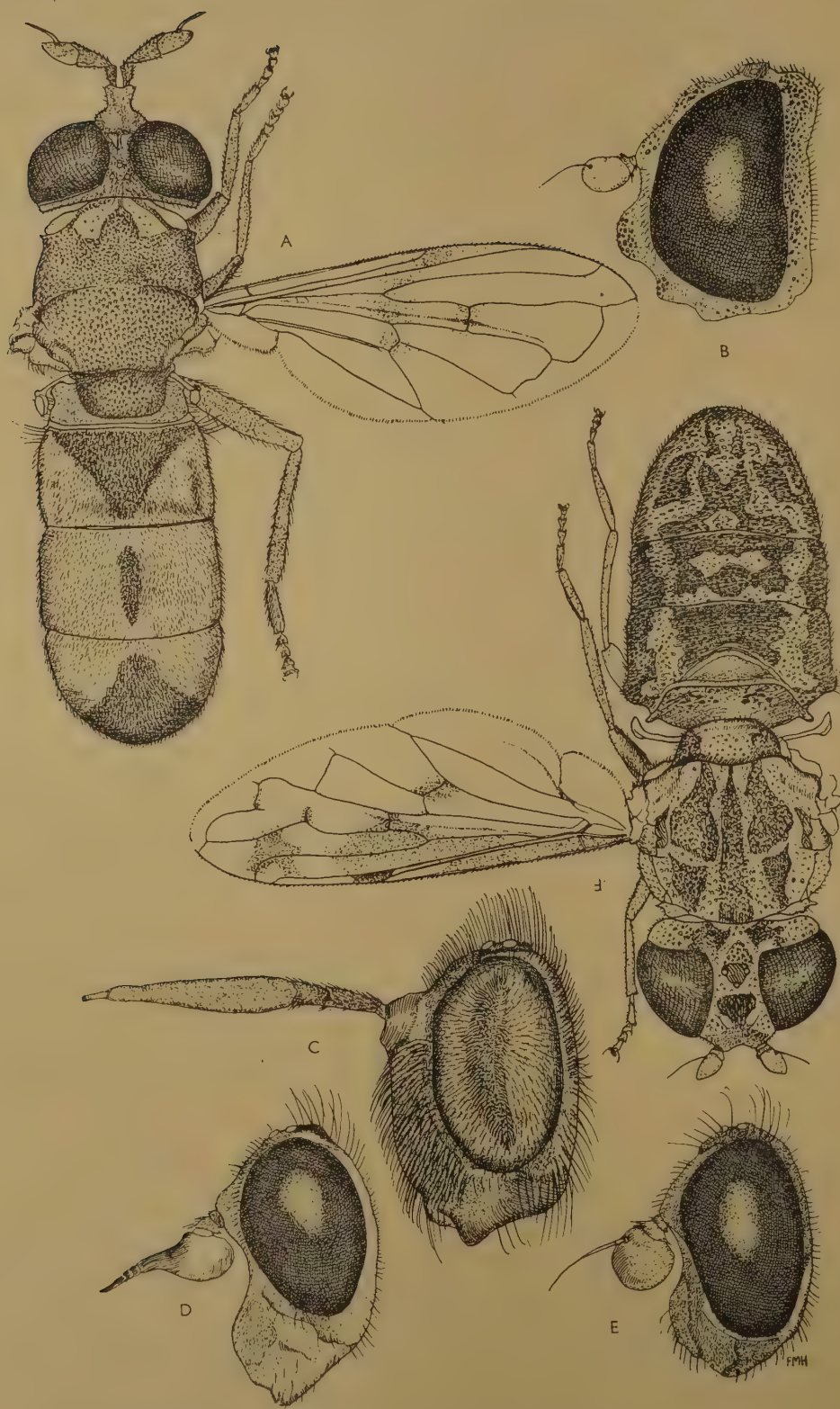
## PELECOCERA Meigen.

*Pelecocera* Meigen, *Syst. Beschreibung*, **3**, 340 (1822).

The eyes are usually bare. The front is a little more than a fourth as wide as the head. The face projects downward and a little forward. In one species the face projects strongly forward and downward to a rather acute point but never to the extent in *Rhingia* and not much more than in *Eurhimyia lineata*. Face pubescent. The cheeks and lower occiput are usually scantily developed, but may be conspicuous and tumid. The first antennal segment small, the third large and thick, drawn out apically until subtriangular in form; it is usually equipped with a terminal, massive, segmented style. Occiput very concave; its flanges strongly



Fig. 19.



The Subfamilies Psarinae, Nausigasterinae, Calliceratinae, Pelecoceratinae.

- A. *Psarus abdominalis* Fabricius, dorsal view; B. *Nausigaster* sp., profile of head; C. *Callicera auripila* Metcalf, profile of head; D. *Pelecocera latifrons* Loew, profile of head; E. *Chamaesyrrhus willistoni* Snow, profile of head; F. *Nausigaster* sp., dorsal view.

developed. Thorax short pilose, slightly convex, pinched in the middle but less convex posteriorly. Humeri pilose. Calli and scutellum equipped with bristles. No scutellar fringe. Metanotum creased. Abdomen thin, slender, margins rolled. The wings are elongate. The anterior cross-vein is well before the middle of the discal cell. The costa and third vein end at the tip of the wing. Subapical and lower marginal cross-veins of about equal length, neither parallel to wing margin; both may be with a spur. There is considerable variation in the position of the small cross-vein shown in different species. Genotype—*tricincta* Meigen. These flies often have light coloured markings on the abdomen.

Distribution : palaearctic 6 ; nearctic 1.

#### ISCHYROPTERA Pokorny.

*Ischyroptera* Pokorny, *Verh. Zool-bot. Ges. Wien*, **37**, 397 (1897).

The occiput is concave. The first antennal segments are small, the third large, thick, subtriangular. The terminal style long, very thick. Face produced below and forward, but not extraordinarily so. Lower occiput and cheeks are grossly tumid and swollen. The wings have the small cross-vein at the middle of the discal cell; the wing is decidedly short. The junction of subapical cross-vein with the third vein lies well back from the apex, and together with the lower marginal cross-vein is spurred. The ending of the costa is at, or but little beyond, the tip of the wing. Genotype—*bipilosa* Pokorny.

Distribution : palaearctic (Europe) 1.

#### THE SUBFAMILY VOLUCELLINAE.

The flies of this subfamily are often large and frequently metallic. A few species are small, and among the many species of *Volucella* are numerous species groups and types. The antennae are almost always moderately elongate, the elongation confined to the second segment. In *Graptomyza* it may become quite long and pendulous. Arista always plumose except in *Tachinosyrphus*. The abdomen is always short, oval or subcircular; it is frequently inflated and usually convex. The thorax is characteristically equipped with numerous long bristles; the pile is seldom soft and fine; metasternum always pilose. Legs simple, the femora without patches of setae, the hind tibia rounded and slender. The venation is characteristic; the third vein and costa usually end far above the wing apex and the apical cross-vein is strongly recurrent. The radial sector appears to be always equipped with numerous long bristles; the stigmal cross-vein is almost never present but it appears to be frequently in process of origin; sixth vein concave on posterior side; the small cross-vein is always before the middle of the discal cell.

The Volucellinae are practically world-wide in distribution except that none are definitely known from the Ethiopian region. *Graptomyza* seems to replace *Volucella* in Africa and Australia, the two overlapping in their range in the East Indies and southern Asia. The neotropical region seems to be the centre of differentiation of this subfamily, where the species of *Volucella* are exceptionally abundant and where several subgenera are found.



The Volucellinae shows strong relationship to the Cheilosinae. The bristly chaetaceous aspect is paralleled in *Cheilosia*, *Ferdinandea*, *Brachyopa*, *Hammer-schmidtia*, as well as the sometimes luteous coloration in the latter genera. The type of face in *Volucella*, often tuberculate, often conate, reminds one of the deep-faced *Cheilosia*, the plumose arista suggests *Hiatomyia*, and *Copestylum* parallels *Taeniochilosia*. Finally *Cheilosia* with its home in the holarctic area, like *Volucella*, has the radial sector strongly bristled.

Two tribes are here recognized. One is the Volucellini; the other the Graptomyzini.

The subfamily may have been differentiated in the Oligocene. The author places the genus *Ptilocephala* (genotype *volucelloides*) from the Baltic amber deposits here. This fly has all the characters of *Volucella* except in the wing, where the venation would pass for *Cheilosia*. Its face and antennae and thorax are characteristically like *Volucella*. It appears to be closer than any Recent form, to the hypothetical ancestral type. Loew mentioned a *Volucella* from Baltic amber but did not describe it; it may have been *Ptilocephala*, or may have been a more modern type. The subfamily contains two tribogenera, one other genus, eight subgenera; *Tachinosyrphus* is perhaps a phylogeront.

*A key to the groups of the Volucellinae,*

1. Arista bare, face much swollen and tumid; abdomen bristly;  
Tachinid-like flies ..... *Tachinosyrphus* Hull.
- Arista at least short plumose, almost always long plumose; rarely  
bare ..... 2
2. Eyes with scale-like hairs standing upright on the surface. .... *Lepidopsis* Curran.
- Eyes bare to pilose, never with scales on their surface ..... 3
3. Apical cross-vein always recurrent as it joins the third longitudinal  
vein ..... 5
- Apical cross-vein usually joining the third vein at right angles;  
sometimes a little curved backward. Small flies with very long  
bristles on thorax and scutellum. Arista short to long plumose.  
Face short to extremely conical. Wings without any trace of the  
vena spuria. Scutellum usually with a concavity on its surface.  
Sides of abdomen strongly convex ..... 4
4. Face jutting forward or downward; third segment of antennae  
elongate ..... *Graptomyza* Wiedemann.
- Face obtuse, very little produced. Third segment of antennae  
almost round, large, subquadrate. .... *Protograptomyza*, subg. n.
5. Antennal arista with very thick feather-like pile ..... 6
- Antennal arista with long loose rays. Loosely plumose or some-  
times bare ..... 7
6. From the dense arisal pile emerge long isolated hairs. Tip of arista  
bare ..... *Volosyrpha* Shannon.
- Aristal pile entirely feather-like, very dense; of uniform length and  
extending to the tip ..... *Copestylum* Macquart.
7. Scutellum with weak tubercular swellings or with a strong median  
swelling ..... 8
- Scutellum normal in shape, or with a pre-apical concavity or flattened. 9
8. Three weak swellings on the scutellum bearing heavy pile. Female  
vertex protuberant ..... *Apophysophora* Williston.
- A single very strong median tubercle situated on the scutellum. .... *Viereckomyia* Curran.

9. Face tri-tuberculate, a median swelling and another on either side of the face. Always in known species metallic greenish or bluish. *Ornidia* Fabricius.  
Face smooth in surface; occasionally metallic, but usually some other colour ..... 10
10. Arista pectinate, with long rays above and extremely short hairs below. Third antennal joint long ..... *Volucellosia* Curran.  
Arista plumose or bare. Ventral arisal hairs at least easily visible. 11
11. Front very long; longer than the face. Eyes of male widely separated. Small metallic species. Hairs of arista sparse and retrorse ..... *Megametopon* Giglio-Tos.  
Eyes of male contiguous. Front not excessively long. Both metallic and non-metallic species ..... 12
12. Small species, frequently pallid in colour, with a concavity on the pre-apical surface of the scutellum, and bristles on the thorax. Submarginal cell usually open ..... *Phalacromyia* Rondani.  
Both large and small species. Scutellum without any trace of concavity. Bristly or bare. Submarginal cell open or closed... *Volucella* Geoffroy.

## VOLUCELLA Geoffroy.

*Volucella* Geoffroy, *Hist. Insect. environs Paris*, 2, 540 (1764).

Small to large flies of wide, inflated abdomen, often nearly circular. Head produced downward, sometimes considerably downward and rarely forward. The face is usually concave above, with either a large rounded tubercle below, or a rounded protuberant bulge, merging on into the epistoma. Eyes holoptic, either bare or pilose. The third segment of the antennae is moderately elongate and sometimes concave. Arista always plumose. The front may be sometimes swollen and inflated. Thorax and scutellum with numerous bristles. Legs simple. Venation characteristic. Marginal cell closed, the apical cross-vein strongly recurrent; together with the third vein and costa, they end far above the top of the wing. Genotype—*Musca pellucens* Linnaeus.

Distribution: palaearctic 20; nearctic 27; neotropical 219; Ethiopian 1 (probably belongs elsewhere); oriental 17; holarctic 1.

Recognized subgenera:

*Copestylum* Macquart (subgenus), *Dipt. Exot. Suppl.* 1, 124 (1846).

These are flies in every way like *Volucella* except in one respect. The arisal pile is entirely feather-like, very dense, of uniform length, and extends to the tip. Subgenotype—*Volucella marginatum* Say.

Distribution: nearctic 4; neotropical 7.

There is no gainsaying the fact that these flies are unique in respect to their arista, nor do we find overlapping forms. The question is, shall all Syrphids, differentiated upon the basis of a unique type of arista alone, be ranked as genera or subgenera? The arista of *Taeniochilosia* Oldenberg is in every respect equally unique. Yet, shall it be regarded as more than a subgenus of *Cheilosia* at best?

*Lepidopsis* Curran (subgenus), *Ann. Mag. Nat. Hist.* (9) 16, 247 (1925).

Small, *Volucella*-like flies; the eyes have scale-like hairs standing upright upon the surface. Subgenotype—*compactus* Curran.

Distribution: neotropical 2.



*Volosyrpha* Shannon (subgenus), *An. Mus. Nat. Hist. B. Aires*, **34**, 575 (1929).

Large species of *Volucella*, in which the arista is densely short plumose, above and below, with a series of larger, pectinate hairs. Genotype—*Volucella hirtipes* Macquart.

Distribution : neotropical 1.

*Viereckomyia* Curran (subgenus), *Ann. Mag. Nat. Hist.* (9) **16**, 243 (1925).

Large, dark, *Volucella*-like flies, in which the scutellum bears a single, strong, median tubercle. Subgenotype—*Volucella gibbera* Schiner.

Distribution : neotropical (Colombia) 1.

*Ornidia* Fabricius (subgenus), *Encycl. Methodique*, **10**, 786 (1825).

Medium-sized, *Volucella*-like flies of brilliant metallic red, green, or bluish green, in which the face bears a pair of additional tuberculate swellings on either side of the median of tubercle, margined by a crease. Subgenotype—*Syrphus obesa* Fabr.

Distribution : neotropical 4.

*Volucellosia* Curran (subgenus), *Amer. Mus Novit.* **413**, 5 (1930).

Medium-sized, *Volucella*-like flies in which the arista is pectinate, with long rays above and very short, dense hairs below. Subgenotype—*Volucella fornax* Townsend.

Distribution : nearctic 1.

*Apophysophora* Williston (subgenus), *Trans. Amer. Ent. Soc.* **15**, 276 (1888).

Small, dark flies in which the scutellum bears three weak swellings beset by heavy pile. The female vertex is somewhat protuberant. I can see no other distinction from *Volucella*. Subgenotype—*scutellata* Will.

Distribution : neotropical (Brazil) 1.

*Phalacromyia* Rondani (subgenus), *Truqui, Studi Entomol.* **1**, 67 ; Pl. III, 1 (1848).

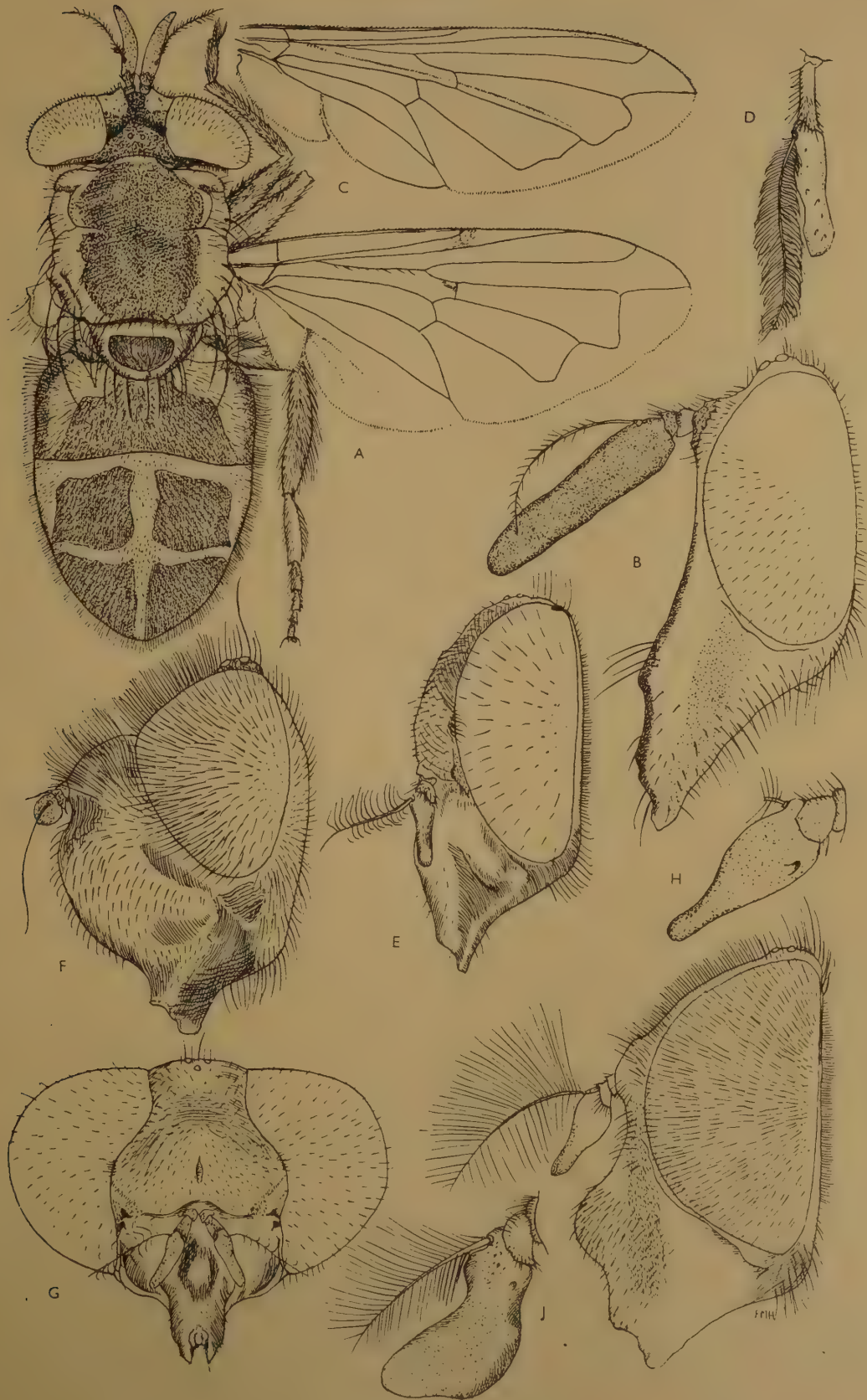
Small species of *Volucella* with the submarginal cell open and usually with a sunken depression just before the apex of the scutellum. These flies are often pallid and luteous but many species are metallic. The author has not seen the genotype and cannot state if the genotype itself has the pre-apical depression. There are annectant forms in which the submarginal cell is closed in the costa. Subgenotype—*submetallica* Rondani.

Distribution : neotropical only ; 26 or more species. Numerous species fall in this division.

#### The Subfamily Volucellinae.

- A. *Graptomyza ventralis* Wiedemann, dorsal view ; B. *Graptomyza ventralis* Wiedemann, profile of head ; C. *Volucella* (*Phalacromyia*) *bipunctata* Hull, wing (paratype) ; D. *Copestylum marginatum* Say, antenna ; E. *Megametopon nasicum* Williston, profile of head ; F. *Tachinosyrphus tachinata* Hull, profile of head (holotype) ; G. *Megametopon nasicum* Williston, front of head ; H. *Volucella chaetogaster* Hull, antenna (type) ; I. *Volucella chaetogaster* Hull, profile of head (type) ; J. *Volucella cockerelli* Curran, antenna.

Fig. 20.





## MEGAMETOPON Giglio-Tos.

*Megametopon* Giglio-Tos, *Boll. Mus. Zool. Anat. Comp. Torino*, **6**, No. 108, 5 (1891).  
*Ophromyia* Williston, *Biol. Cent. Amer. Dipt.* **3**, 55 (1891).

This group rests upon three distinctions. Eyes bare; the eyes of the male are widely dichoptic; the front is very wide, extremely deep and rather flat. The antennae arise but a little way from the bottom of the eyes. Face shallowly concave beneath the antennae, rising to an inconspicuous tubercle, then descending quite straight to a pointed epistoma. Head much broader than the thorax. Bristles of thorax tubercle-set. Abdomen barely longer than broad, not greatly thickened. The first posterior cell has rounded angles and a recurrent cross-vein and the second posterior cell has a sharp angle and a short spur. Third vein ends practically at the tip of the wing; marginal cell closed. Genotype—*Ophromyia nasica* Williston.

Distribution: neotropical (Mexico) 3.

## TACHINOSYRPHUS Hull.

*Tachinosyrphus* Hull, *Proc. Ent. Soc. Wash.* **38**, 167 (1936).

A phylogeront. Dark, medium-sized, chaetaceous species, in which the arista is bare and resembles a shellacked bristle. Eyes holoptic, very long pilose. Face and front bloated, tumid, swollen, with appressed bristly hairs; the contour is round, smooth, dropping to a short, constricted, acute vertical cone. Antennae short; third segment subglobose. Thorax and scutellum *Volucella*-like. Abdomen oval, slightly flattened, very long and densely bristly. Legs quite slender. Venation *Volucella*-like; marginal cell closed. Genotype—*pseudotachina* Hull.

Distribution: neotropical (Peru) 1.

The author has been unable to decide if the arista has been plumose and has lost its plumosity or if this is a primitive member of the subfamily; there is no indication on any of the types that it has been present.

## GRAPTOMYZA Wiedemann.

*Graptomyza* Wiedemann, *Nova. Dipt. Gen.* **16** (1820).

A remote genus. Small flies with wide, short head. Face straight for some distance below antennae, they are produced diagonally forward in a blunt epistomal cone or sometimes into a very acute cone. Antennae a little above middle of eyes; third segment usually quite long and flat, with rounded tip, even paper-thin in cases. Arista long, slender, from long plumose to short plumose or nearly bare. Eyes usually pilose; widely dichoptic; vertex level with eyes or even concave as in Asilids. Front and face varying from narrow to quite wide; front with crescentic creases as in many *Volucella* and *Cheilosia*. Thorax broad, short, chaetate; scutellum with marginal macrochaetae, and often provided with a dish-like concavity before the apex as in *Phalacromyia*. Abdomen particularly curious and interesting; longer than broad, markedly convex, the sides thick and rolled over; the whole appearance suggests Meliponid bees. Apex of abdomen sometimes with a collar-like shield concealing genitalia; posterior margin of first segment often dentate. Hind femora about the middle, their tibiae distally, their basitarsi a little thickened.

Marginal cell over; third vein ending practically at wing apex; lower and apical cross-veins straight, or curved outward, joining their respective veins at right angles, or even recurrent, in any case far from the apex of wing. Vena spuria completely absent save for a nodal trace. Genotype—*ventralis* Wiedemann.

Distribution: Ethiopian 9; oriental 35; Australian 5; Oceania 1. Szilady erroneously described a species from the West Indies.

Recognized subgenera: *Protograptomyza*, new subgenus.

Those *Graptomyza* with the third antennal segment very large and subquadrate; this face short and obtuse; arista pubescent. Subgenotype—*Graptomyza doddi* Ferguson.

Distribution: Australian 1.

*Ptilocephala* Hull (fossil genus). Characterized by: face deep conical and tuberculate and bristly; scutellum with depression; third antennal segment elongate; arista plumose. First postical cell with a rather long stalk; apical cross-vein joins third vein rectangularly but recurrent. Genotype—*volucelloides* Hull.

#### THE SUBFAMILY SERICOMYINAE.

This is a small group of medium-sized to large Syrphids which are characterized by the short, oval, or even subcircular, convex abdomen and the plumose arista of the short antennae, and the radial sector bristles. The face is short but deeply produced downward and often conate and in general not unlike that of *Volucella*. Indeed, there seems to be a close relationship between these two subfamilies which differ principally in their venation. They have however been placed at times in the Xylotinae and it is possible their relationships are with the Criorrhini. The subfamily contains one tribogenus, two genera, four subgenera (*Arctophila*, *Pseudovolucella*, *Condidea*, *Conosyrphus*). There is comparatively little difference between *Arctophila*, *Conosyrphus* and *Sericomyia* as far as the author can discover.

#### A key to the groups of Sericomyinae.

1. Face very broad, much swollen below, about the epistoma and cheeks. Eyes reduced and densely long pilose. Hind femora quite slender ..... *Pyritis* Hunter.  
 Face is broad, deep conate, or the hind femora massive and arcuate, or the eyes bare ..... 2
2. Third vein deeply curved into the first posterior cell. Face wide, flat, deeply conate ..... *Pararctophila* Hervé-Bazin.  
 Third vein shallowly curved or more usually, nearly straight. Face short or long conical ..... 3
3. Third antennal segment quite truncate; eyes of male widely dichoptic; face quite long and deep, with a weak tubercle above. *Tapetomyia* Fluke.  
 This segment not truncate or the males dichoptic ..... 4
4. Eyes extremely wide and short and flattened in profile from above, the sides rounded. Face deep but rather flat. Hind femora usually much thickened and incrassate. Hind tibiae about three-fifths as long as hind femora, sometimes less ..... *Pseudovolucella* Shiraki.



- Eyes prominent but never greatly flattened ; face, if flattened, extremely deeply produced and conate, the tubercle very small, if face short, the tubercle conspicuous. Hind femora always simple ..... 5
5. Face deeply, vertically conate, flat in profile particularly beneath the antennae. Tubercle small and inconspicuous ..... 6
- Face produced below eyes but never deep conically ; beneath the antennae somewhat concave. Facial tubercle apt to be prominent. 7
6. Abdomen very flattened, especially in the female. Bare upon the abdomen ..... *Conosyrphus* Frey.
- Abdomen convex in both sexes. Usually very long erect pilose, sometimes shaggy only on the terminal segments ..... *Arctophila* Schiner.
7. Third vein with a shallow loop into first posterior cell ; facial tubercle conspicuous, abdomen with pairs of spots ..... *Condidea* Coquillett.
- Third vein if curved at all, barely curved over its whole length as in some species of *Syrphus*. Facial tubercle not very conspicuous . *Sericomyia* Meigen.

#### SERICOMYIA Meigen.

*Sericomyia* Meigen, *Illiger's Mag. f. Insektenkunde*, 2, 274-79 (1804).

The head is about as wide as the thorax. Eyes usually bare, touching for a short distance in males. Vertical triangle small and protuberant. Face below the antennae shallowly concave over a long distance, dropping down to a low tubercle which is below the eyes ; the face then descends abruptly. Occiput thick below, narrow above. Antennae short ; third segment barely longer than wide and subtruncate apically ; the short arista plumose. The scutellum is large, semicircular, convex, with a long, copious ventral fringe ; metasternum long pilose. The abdomen is very broad, but little longer than wide and convex. The hind femora are slender or but little thickened. Upon the wings the anterior cross-vein is oblique and enters the discal cell barely before the middle ; third vein and costa end a little before the tip of wing ; marginal cell broadly open ; vena spuria faint. The genus contains large, dark, rather pilose flies, especially upon the thorax, in which the abdomen is usually fasciate with yellowish bands or spots. Genotype—*Musca lappona* Linnaeus.

Distribution : palaearctic 10 ; nearctic 9 ; oriental 4 ; holarctic 1, or possibly 2.

Recognized subgenera : *Conosyrphus* Frey, *Mem. Acad. Sci. Petrograd* (8) 29, 10-18 (1915).

The only distinction I can find, upon study of the genotype, is the somewhat flattened abdomen of the female, which is short pilose in contrast to the rather long pile of most members of the genus *Sericomyia*. It is true the facial cone is remarkably deep, the tubercle perhaps even smaller. None of these characters deserve great weight. Subgenotype—*tolli* Frey.

Distribution : palaearctic 1.

*Condidea* Coquillett (subgenus), *Canad. Ent.* 39, 75 (1907).

Very much like *Sericomyia*. The third vein has a shallow loop into the first posterior cell ; the facial tubercle is more conspicuous, the paired spots of the abdomen present a characteristic facies. There are no characters of much value. Subgenotype—*lata* Coquillett.

Distribution : nearctic 3.

*Arctophila* Schiner (subgenus), *Wien Ent. Mschr.* **4**, 215 (1860).

These are large, dark, long pilose flies, in general quite similar to *Sericomyia* except that they lack the paired spots and fascia of yellow. Like that genus, the abdomen is short and convex. The sole difference appears to lie in the fact that the face is considerably longer and deeper, and of the low tubercle there only remains a trace. These are distinctions no greater than those found on the face of various species of *Volucella*, or *Cheilosia*. There are numerous minor variants in the two genera. In the genotype and in *mussitans*, *harveyi* and *S. militaris* the hind femora are considerably thickened and arcuate (stoutest in genotype). In the genotype the third vein is very shallowly curved downward over nearly its whole length, precisely as again seen in *S. militaris* and *borealis*, but in *A. mussitans*, *harveyi* and *S. chrysotoxoides* it is quite straight. In *A. flagrans* there is a shallow but definite loop. Finally, in the two European species of *Arctophila* and in *S. borealis* and *chrysotoxoides*, the third antennal segment is rounded, whereas it is markedly truncate in *A. harveyi* and *S. militaris*, and again in *Pararctophila oberthuri*, with its deep loop and recurrent apical cross-vein. This survey of the characters of the four species of each group, including the genotypes, should show how closely inter-related are these flies. The American species of *Arctophila* seem intermediate between the two groups. Genotype—*Syrphus bombiformis* Fallen.

Distribution : palaearctic 3 ; nearctic 2 ; oriental 1.

*Pararctophila* Hervé-Bazin (subgenus), *Insecta*, **4**, 152 (1914).

*Syngenicomyia* Becker, *Mitt. Zool. Mus. Berl.* **10**, 88 (1921).

Very compact, short abdomen species not differing from *Arctophila* except in the deeper loop of the third vein, and the more slender hind femora. The third segment of the antennae is truncate. Becker's genotype of *Syngenicomyia* was *pellicea*, a synonym. Genotype—*oberthuri* Hervé-Bazin.

Distribution : palaearctic 1.

*Bulboscrobia* Gauntitz (subgenus), *Ent. Tidskr.* **58**, 91 (1937).

This form I place as a subgenus of *Sericomyia*, based entirely upon the oblique furrows which, the author states, stand out upon the second, third and fourth abdominal segments. The author further stated that the scanty abdominal pile was closely appressed, but this is purely a specific character. No further description is given. Not studied. Subgenotype—*undulans* Gauntiz.

Distribution : South Sweden.

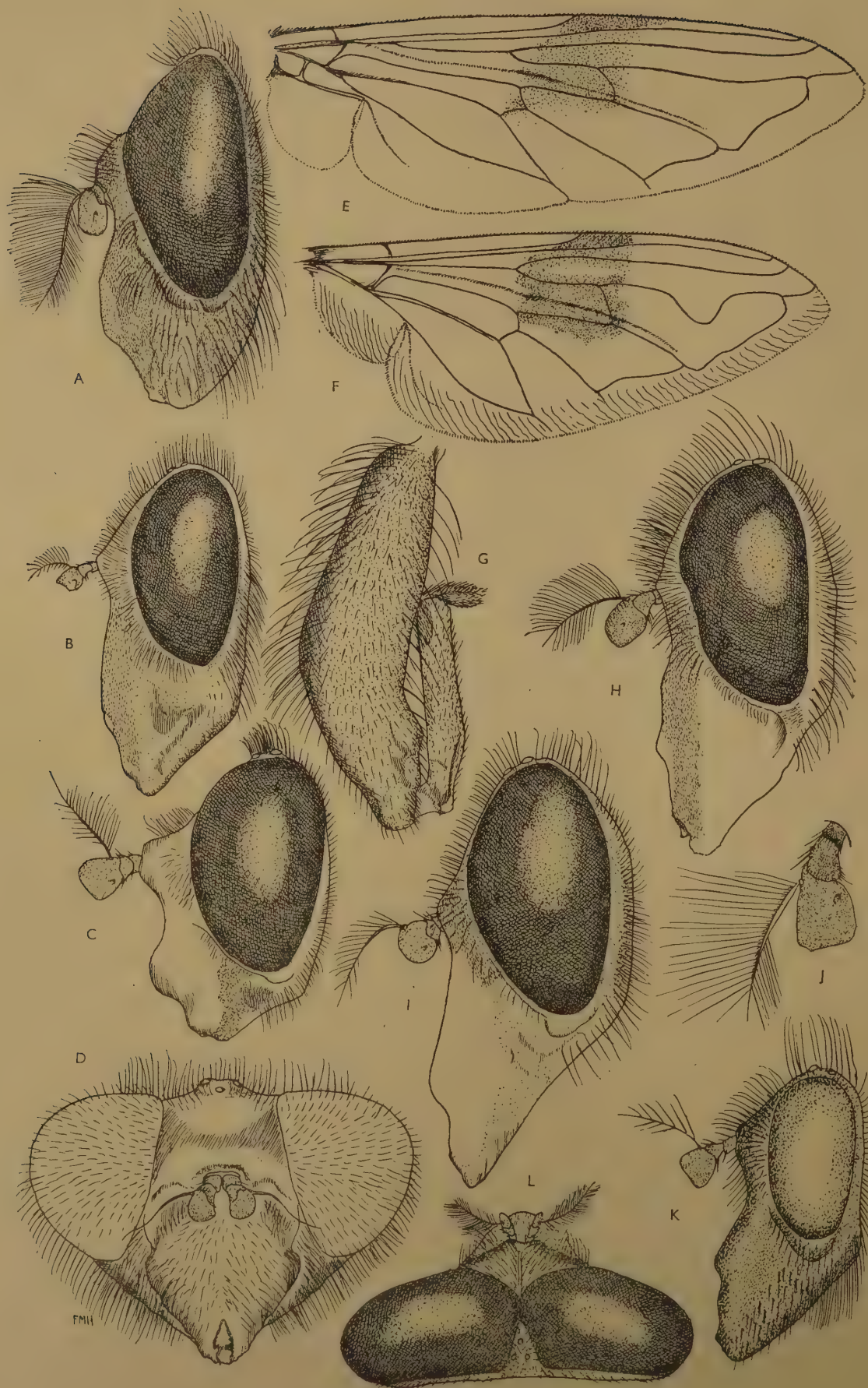
#### PSEUDOVOLUCELLA Shiraki.

*Pseudovolucella* Shiraki, *Mem. Fac. Sci. Agric. Taihoku*, **1**, 40 (1930).

In these dark coloured, large *Sericomyia*-like flies the face is deep and long, but not so conical as in *Arctophila*. There are wide, well differentiated facial stripes ; head is quite wide ; eyes short but very wide ; third segment of the antennae is longer than wide, its apex rounded ; the arista bears thirty-five to forty long, close-set plumes, its relatives with only about half as many. Hind femora greatly thickened and arcuate, though perhaps no more than in *Arctophila bombiformis*, but their tibiae are greatly shortened. Finally the third vein is quite or practically



Fig. 21.



straight, with the apical cross-vein ending in third vein far from the wing apex, but not recurrent. Like *Pararctophila* the head is triangular from in front. Genotype—*mimica* Shiraki.

Distribution : palaearctic 1 ; oriental 6.

#### PYRITIS Hunter.

*Pyritis* Hunter, *Canad. Ent.* **29**, 131 (1897).

Long pilose, dark, medium-sized flies with wide, triangular, swollen head ; eyes reduced in size and densely pilose, holoptic in males. The front is very broad in the female. Antennae are short, third segment about as wide as long and rounded ; arista short, thick plumose. Below the antennae the face is shallowly concave, dropping to a broad rounded tubercle below or just opposite the lower part of the eyes. The face from the front is extremely wide, flat and swollen, much produced below the eyes, and the facial stripes excessively wide, and deep-creased and pilose. Occiput massive and tumid. The front, vertex, occiput and cheeks are densely, long, shaggy pilose. Scutellum with a ventral fringe. The abdomen is a little longer than wide. Hind femora very slender ; moderately arcuate. The submarginal cell of the wing is widely open, third vein straight, ending with costa a little before tip of wing ; apical cross-vein joins third vein far from the apex, but is not recurrent ; anterior cross-vein oblique, entering the vein quite at middle of the discal cell. Genotype—*montigena* Hunter.

Distribution : nearctic 2.

#### TAPETOMYIA Fluke.

*Tapetomyia* Fluke, *Ann. ent. Soc. Amer.* **32**, 370 (1939).

Large flies, thick and long pilose like bumble-bees. Face very deeply conical with a small tubercle below the bottom of the eyes ; face concave above the tubercle. Antennae short, the third segment short and quite truncate ; arista sparsely plumose, the ventral rays shorter and fewer. Males holoptic ; eyes bare ; ocelli equidistant. Abdomen oval. Hind femora slender and straight. Third vein with a slight curve into the first posterior cell ; this cell with a rather long petiole and the last third of the apical cross-vein recurrent ; marginal cell open ; the oblique anterior cross-vein is beyond the middle of the discal cell. Not studied by the author. Genotype—*meyeri* Fluke.

Distribution : neotropical (Mexico) 1.

---

#### The Subfamily Sericomyninae.

- A. *Pseudovolucella apimima* Hull, profile of head (holotype) ; B. *Pararctophila oberthuri* Hervé-Bazin, profile of head ; C. *Condidea lata* Coquillett, profile of head ; D. *Pyritis kincaidi* Hunter, front of head ; E. *Pseudovolucella apimima* Hull, wing (holotype) ; F. *Pararctophila oberthuri* Hervé-Bazin, wing ; G. *Pseudovolucella apimima* Hull, hind femur and tibia (holotype) ; H. *Arctophila bombiformis* Fallen, profile of head ; I. *Conosyrphus tolli* Frey, profile of head ; J. *Pararctophila oberthuri* Hervé-Bazin, antenna ; K. *Tapetomyia meyeri* Fluke, profile of head (redrawn from Fluke) ; L. *Pseudovolucella apimima* Hull, dorsal view of head (holotype).



## THE SUBFAMILY XYLOTINAE.

This is a large and diverse subfamily. It appears to be related to the Cheilosinae on the one hand, and upon the other somewhat less closely to the Eristalinae. These flies are best characterized by the general position of the anterior cross-vein which, with few exceptions, lies at or beyond the middle of the discal cell. In addition to this, the form is usually elongate, though rarely petiolate, the arista is simple, the marginal cell usually open, and the straight or curved third vein is rarely looped. The fact that the subfamily has developed in several directions adds to the difficulty of easily characterizing it. The femora usually have patches of setae basally upon the first or first and second pairs of legs but not upon the third; rarely a faint trace may be detected on the hind pair. The hind tibiae are frequently knife-like basally and their femora ridged below. A stigmal cross-vein is rarely present. It does not seem that the character of the pile on the metasternum can be used as a main line of cleavage to separate the groups of the subfamily. Of forty-two genera which I have been able to check for this character, eighteen have the metasternum pilose (as well as usually pubescent) and one is variable. In at least two instances pile seems to be present without pubescence. *Criorrhina*, *Eriophora*, *Deineches*, *Merapioidus* are pilose; *Crioprora*, *Pocota*, *Hadromyia*, *Cynorhina* are pubescent, *Neplas* and *Xylotomima* are pilose. On the other hand related groups may be thrown together. *Crepidomyia*, *Tatuomyia*, *Ceriogaster*, *Senoceria*, *Mutillimya*, *Cacoceria* are all pubescent, and *Syritta*, *Tropidia* and *Nepenthosyrphus* are all pilose. In any event we must fall back on other characters for categories such as tribal distinctions.

Several tribes may be recognized. First, the Xylotini; these are short pilose, setaceous species with the face concave, the femora either slender or greatly swollen and the abdomen sometimes petiolate. Second, the Temnostomini; large, wasp-like, usually bright yellow pollinose, the femora simple, the anterior cross-vein at or near the middle of the discal cell. Third, the Milesini; large flies with front more or less produced, the face concave, or plano-concave, the marginal cell closed, or open, the femora slender and often toothed. Fourth, the Criorrhinini; large, shaggy, woolly, usually long pilose flies, the face generally tuberculate, the metasternum pilose; *Lycastris* possibly belongs here, or by itself. Fifth, the Pocotini, in which the metasternum is pubescent and the face concave, and which are also rather long pilose as a rule. Lastly the Tropidini, in which the face is distinctly tricarinate. The most aberrant flies in this subfamily seem to be the phylogeronts *Lycastris* and *Nepenthosyrphus*. The author has disposed the groups into the six tribogenera; twenty-one genera (six of which are remote and highly specialized), sixteen subgenera, and two *Takaomyia* and *Odyneromyia*, here regarded as members of Cheilosinae have also been included in the key to the Xylotinae, in order to make certain of their determination by the student.

*A key to the groups of the subfamily Xylotinae.*

1. Face drawn out into a long, conical, porrect snout ending far beyond the antennae. Subcostal cell of wing with numerous extra cross-veins. Metasternum pubescent ..... *Lycastris* Walker.  
 Face usually not snout-like; if drawn out into an epistomal projection it is scarcely as long as the antennae. Subcostal cell never with extra cross-veins and usually with none ..... 2

2. Face tricarinate; hind femora swollen, sometimes greatly enlarged (Tropidini) ..... 12  
     Face never with a well-developed medial keel and lesser face-cheek keels ..... 3
3. Third antennal segment definitely deeper than long, the dorsal arista subbasal; large, thickly long pilose flies ..... 4  
     Third segment either orbicular or elongate; almost exclusively short pilose; rather bare groups of flies ..... 5
4. Metasternum pilose, face concave above, tuberculate below, the tubercle often small (Criorhinini) ..... 17  
     Metasternum pubescent. Face concave (Pocotini) ..... 21
5. Anterior cross-vein quite oblique and carried far out towards the end of the discal cell, to the last sixth of its length; cubital cell with a very long petiole drawn out along wing margin. Very large flies, often brightly marked (Milesini) ..... 27  
     Anterior cross-vein less oblique, entering the third vein but little beyond the middle of the discal cell; cubital cell with a short, straight petiole ..... 6
6. First and especially the second antennal segments elongated; second segment usually longer than the third (Temnostomini) .. 29  
     First and second segments short ..... 7
7. Bright, yellow pollinose, wasp-like flies, extensively covered with pollen; pile sparse, or petiolate species with the anterior wing border brown (Temnostomini) ..... 29  
     Dark or metallic flies, never yellow pollinose, rarely marked with yellow ..... 8
8. Face short and convex, retreating; hind femora exceptionally, massively enlarged; abdomen short, small, subcylindrical; metasternum pilose ..... *Nepenthosyrphus* de Meijere. 9  
     Face never convex and retreating ..... 9
9. Metasternum pubescent only. Frontoantennal region prominent, especially dorsally; face high, plano-convex, or slightly concave above, nearly straight in profile ..... 33  
     Face usually concave; or if frontoantennal region is prominent, the face is retreating or deeply concave, metasternum either pilose or pubescent ..... 10
10. Face below very short and markedly retreating below the antennae. Face in the middle with a small tubercle ..... *Macrozelima* Stackelberg. 11  
     Face not usually short and retreating; with a small tubercle ..... 11
11. Face with a strongly developed protuberant tubercle near the middle, concave above; face projecting rather deeply downward; metasternum pilose; scutellum bituberculate; hind femora with a subapical plate ..... *Malometasternum* Shannon. 34  
     Face concave; third antennal segment often elongated (Xylotini). 34
12. Hind femora with a prominent, subapical, lateral plate often bearing one or two blunt teeth; abdomen elongate but tapered and quite convex apically; abdomen never constricted basally ..... 16  
     Hind femora without such plate, but usually strong tuberculate spines ..... 13
13. Abdomen coarctate; strongly constricted basally ..... 14  
     Abdomen scarcely or not at all constricted ..... 15
14. Second abdominal segment apically wider than the base of the abdomen; hind tibiae with only a single tooth ..... *Senoceria* Hull.



- Second segment narrower than base of abdomen, long and slender ;  
hind tibiae bidentate ..... *Tatuomyia* Shannon.
15. Abdomen rather flattened and practically without any trace of  
constriction ; medium to large flies ..... *Crepidomyia* Shannon.  
Abdomen definitely petiolate, small flies ..... *Ceriogaster* Williston.
16. Whole face immediately jutting forward beneath the antennae, from  
whence the straight face drops vertically downward ..... *Ortholophus* Bigot.  
Face not jutting out beyond base of antennae ; keel vertical and  
straight or slightly convex ..... *Tropidia* Meigen.
17. Third antennal segment pyriform and unusually deep, much shorter  
than long, the peaked dorsal apex bearing the arista. Hind  
femora slender ..... *Merapioidus* Bigot.  
Third antennal segment not unusually short and pyriform ..... 18
18. First and second antennal segments elongate, each about as long as  
the third ; third antennal segment longest ventrally ; abdomen  
short, subcircular, face deeply produced, eyes pilose ; small cross-  
vein oblique, entering the fourth vein at distal fourth of the discal  
cell ; third vein concave anteriorly, the confluence with apical  
cross-vein back from end of wing. Face retreating below the  
large, low tubercle placed in the middle of the face ..... *Nosodepus* Speiser.  
First and second antennal segments not elongate ; third segment  
usually short ventrally ..... 19
19. Hind femora thickened throughout with blunt, apical, obtuse tooth ;  
eyes bare ; third vein and apical cross-vein meet quite at the wing  
apex, the last section of the first posterior cell drawn out quite  
narrowly ; apical cross-vein long and oblique, entering fourth vein  
at the distal fifth of the discal cell ; abdomen elongate ..... *Deineches* Walker.  
Hind femora without apical tooth ; third vein and apical cross-vein  
usually meet some distance back from the apex, last section of  
first posterior cell not unusually narrow ..... 20
20. Abdomen subcircular, wider than thorax ; hind femora simple ;  
third antennal segment longest ventrally and obliquely rounded  
above, the ventral apex rounded ; anterior cross-vein meets discal  
cell at its middle ; head quite wide ; face without pile upon the  
sides ..... *Eriophora* Philippi.  
Abdomen more elongate ; hind femora simple or enlarged ; third  
antennal segment short above and below ; face at least usually  
pilose, sometimes with mystax above the epistoma ; anterior  
cross-vein meets discal cell near discal fourth ..... *Criorrhina* Meigen.
21. Eyes thickly pilose, wing slender, the first posterior cell and the  
apical cross-vein quite long ; third antennal segment longest  
ventrally, sides of face thickly pilose ; femora simple ..... *Macrometopia* Philippi.  
Eyes bare ; sides of face without pile except upon the strips ;  
pubescence may be present ..... 22
22. Upper face and front drawn out into a long, conical prominence ;  
face concave ; femora slender ..... *Calliprobola* Rondani.  
Upper face and front not unusually prominent ..... 23
23. Face concave, drawn out below, both downward and forward, and  
laterally compressed ; anterior cross-vein near middle of discal  
cell and nearly transverse ; hind femora greatly enlarged ; tibiae  
excavated ; face without pubescence ..... *Crioprora* Osten-Sacken.  
Face not laterally compressed, drawn out ..... 24

24. Face quite concave, the epistoma projecting as far forward as the front ..... 25  
 Face retreating, the epistoma scarcely produced; hind femora but little thickened, the thickening greatest in the middle, sides of face bare; lower half of front bare ..... *Philippimyia* Shannon.
25. Front long pilose, face pubescent. Hind femora greatly enlarged, with blunt tooth at apex and tibia excavated basally; third vein and apical cross-vein confluent some distance from wing apex ... *Brachypalpus* Macquart.  
 Male front bare or pubescent only, female front bare on lower half; femora simple, or but little thickened ..... 26
26. Third vein and apical cross-vein confluent some distance from wing apex; male middle femoral base with very long curved spur ... *Hadromyia* Williston.  
 These veins confluent quite at the wing apex; no spur ..... *Pocota* St. F. and S.
27. Hind femora slender, with an apical tooth. Eyes with vertical irregular stripes, or blotches. Metasternum with an obtuse blunt spur anteriorly. First and second antennal segments more or less elongated; bright, wasp-like flies ..... *Spilomyia* Meigen.  
 Hind femora often thickened, with or without tooth. Eyes uniform. No metasternal tooth. Antennae scarcely or not at all elongated. 28
28. Marginal cell closed; face usually concave and the front produced; apical cross-vein and third vein confluent at apex, or back from apex of wing ..... *Milesia* Latreille.  
 Marginal cell widely open; third vein with a spur at the bottom of the shallow concavity; third vein and apical cross-vein confluent far back from apex; face and front both long, but face nearly straight and vertical ..... *Pogonosyrphus* Malloch.
29. First and second segments of antennae elongated; abdomen constricted basally and deep, face vertical with a small tubercle in the middle; hind femora greatly thickened beyond the basal fourth, with three spines; anterior cross-vein before the middle of the discal cell; metasternum pubescent ..... *Cacoceria* Hull.  
 First and second segments of antennae elongate or short; if elongate, the abdomen is never constricted ..... 30
30. Abdomen constricted and strongly petiolate; face concave, anterior margin of the slender wing brownish; antennae short; metasternum pubescent ..... 31  
 Abdomen not constricted; black and bright yellow pollinose wasp-like flies; metasternum pilose ..... 32
31. Male narrowly dichoptic; alula of wing narrow. Confluence of apical and third veins back from apex of wing; antennae short . *Takaomyia* Hervé-Bazin.  
 Male narrowly holoptic, with a small tubercle near epistoma ..... *Odyneromyia* Shannon.
32. First and second antennal segments usually lengthened, often greatly elongate. Third segment occasionally deeper than long. Face usually vertical, barely or but little concave; face deeply produced: *Sphecomyia* Latreille.  
 First and second segments always quite short; face usually quite concave especially in females, less so in males; males often with a weak tubercle; face never deeply produced; metasternum apilose in a few species ..... *Temnostoma* St. F. and S.
33. Frontoantennal region greatly produced; face deep, nearly straight, slightly concave; third antennal segment orbicular; confluence of third and subapical cross-vein back from apex ..... *Somula* Macquart.  
 Front not or scarcely produced; face usually rather concave, especially below the antennae, the lower face prominent; confluence of third and apical cross-vein either at apex or back from the apex of the wing ..... *Cynorhina* Williston.



34. The simple hind femora bear a projection with double tooth ; whole upper half of face together with lower front produced and conical ; face concave ; anterior cross-vein very oblique with a long distal branch. Large, compact flies, abdomen quite short ; metallic . . . *Stilbosoma* Philippi.  
Hind femora without bifid plate, or the cross-vein without branch 35
35. Abdomen greatly constricted upon the second segment, expanded again before its apex ; third antennal segment longer than wide and subtruncate ; femora simple ; eyes of male narrowly touching. Abdomen not constricted, or if so, more than one segment is involved. *Mutillimya* Hull. 36
36. Epistoma greatly produced either forward or downward . . . . . 37  
Epistoma not greatly produced . . . . . 38
37. Face jutting forward . . . . . *Rhinotropidia* Stackelberg.  
Face produced obliquely downward, and quite concave above . . . . . *Paratropidia* Hull.
38. Third vein with a deep kink, large flies with concave face and third antennal segment elongate ; marginal cell widely open . . . . . *Syrittosyrphus* Hull. 39  
Third vein sometimes elongate concave ; never with a kink . . . . .
39. Hind femora with a bifid plate near apex ; abdomen of male strongly constricted between base of second and end of third segments, both laterally and dorsoventrally ; apex of abdomen and hypopygium form an oval club ; the flattened less constricted female abdomen with a pair of large bullae upon third and fourth segments . . . . . *Senogaster* Macquart. 40  
Hind femora without a bifid plate or abdomen without bullae . . . . .
40. Face weakly carinate or with an obtuse, longitudinal ridge ; never with a keel . . . . . 41  
Face not carinate or ridged . . . . . 43
41. Face retreating strongly ; hind femora slender, scarcely thickened ; large metallic flies ; face wholly pubescent . . . . . *Sterphus* Philippi.  
Face always concave, the epistoma produced ; hind femora always much thickened . . . . . 42
42. The spines of the femora mostly borne on an apical, lateral plate or ridge ; pollinose-marked flies ; abdomen generally a little narrowed apically ; scutellum without a ventral fringe ; last section of apical cross-vein rectangular to third vein ; epistoma sometimes produced. *Syritta* St. F. and S.  
No plate or ridge apically upon the femora ; not pollinose flies ; scutellum with a ventral fringe ; last section of apical cross-vein oblique ; metallic flies . . . . . *Neplas* Porter.
43. Metasternum pilose . . . . . 45  
Metasternum pubescent . . . . . 44
44. Posterior margins of the segments with thick matted borders of pile ; large, aeneous or cupreous flies with dense pile of medium length. *Chrysosomidia* Curran.  
Posterior margins not with conspicuous matted borders ; less strikingly metallic flies, with shorter pile and usually smaller . . . *Xylota* Meigen.
45. Hind femora compressed below on distal third or more into narrow spiniferous ridges . . . . . 46  
Hind femora rounded below ; without ridge . . . . . 47
46. Abdomen constricted between second and third segments ; hind femora curved inward on the distal half ; their tibiae quite arcuate. *Cheiroxylota*, subg. n.  
Abdomen not constricted basally ; hind femora straight though much thickened . . . . . *Xylotomima* Shannon.
47. Abdomen wide and flattened, but little elongate ; scutellar fringe virtually absent ; hind femora moderately thickened . . . . . [Sacken.  
Abdomen not especially widened and flattened ; scutellar fringe well developed ; hind femora considerably thickened ; lower portion of face rather compressed laterally, the cheek-face angles distinct . . . . . *Xylotodes* Shannon.

## XYLOTA Meigen.

*Xylota* Meigen, *Syst. Beschreibung*, **3**, 211 (1822).

*Heliophilus* Meigen, *Illiger's Mag. f. Insektenkunde*, **2**, 273 (1803).

These are short pilose, elongate, medium-sized to small flies which are often metallic. Antennae short; the third segment varies from orbicular to a little longer than wide and perhaps occasionally a little wider than long. Face always concave, the lower part well produced diagonally but subtruncate. Face usually pubescent but without pile except upon stripes. Eyes holoptic. Scutellum with ventral fringe; metasternum pubescent. The unarmed hind femora conspicuously slender though often there is a little thickening spread throughout; femora spinose below. While it is true that one or two species may vary with respect to the presence of pile on the metasternum, nevertheless, the great majority of the species fall definitely into the one class or the other; seemingly each group has its closely related variants. Genotype—*Musca segnis* Linnaeus.

Distribution: palaearctic 34; nearctic 44; neotropical 8; Ethiopian 3; oriental 32; Australian 6; holarctic 1.

Recognized subgenera:

*Palaeoxylota*, new subgenus. This name is proposed for those species of *Xylota* which are widely dichoptic in the male. Subgenotype—*Xylota probosca* Hull.

*Xylotomima* Shannon, *Proc. U.S. Nat. Mus.* **69**, No. 9, p. 15 (1926).

Flies very similar in general appearance to *Xylota* but with the metasternum pilose. Subgenotype—*Xylota vecors* Osten-Sacken.

Distribution: palaearctic 1; nearctic 12; holarctic 1; some of the European species credited to *Xylota* may belong here.

*Macrozelima* Stackelberg, *Konowia*, **9**, 224 (1930).

Similar to *Xylota*. Hind femora slender with subapically a medial and lateral dentate spur. Subgenotype—*Macrozelima bidentata* Stackelberg.

Distribution: palaearctic (Japan) 1.

*Cheiroxylota*, new subgenus.

For those Xylotinae flies in which the abdomen is constricted between the second and third segments and the very thick hind femora is curved inward upon the distal half. Hind femora rounded below, without ridge; hind tibiae quite arcuate, rather shortened. Metasternum pilose. Subgenotype—*Xylota dimidiata* Brunetti.

Distribution: Indian 1.

## NEPLAS Porter.

*Planes* Rondani, *Arch. Zool. Anat. Fisiol*, **3**, 9 (1863); preoccupied.

*Neplas* Porter, *Rev. Chil. Hist. Nat.* **31**, 96 (1927).

Metallic species, rather smaller than the average *Xylota*. The concave face is subcarinate at least upon the lower half, without keel. Third antennal segment always elongate. Hind femora below characteristically compressed or pinched



into a spiniferous ridge ; base of their tibiae often knife-like. Hind femora always very greatly thickened. Scutellum with ventral fringe ; metasternum pilose. Genotype—*Xylota vagans* Wiedemann.

Distribution : neotropical 26.

#### BRACHYPALPUS Meigen.

*Brachypalpus* Meigen, *Suite à Buffon*, 1, 523-24 (1830).

Large, elongate, rather long pilose and not very narrow species with quite concave face ; eyes of male narrowly separated. Lower face diagonal, elongate and subtruncate. Scutellum with ventral fringe. Metasternum pubescent. Hind femora elongate and quite thick, though not massive as in *Planes*. First posterior cell with a well-developed petiole. Genotype—*Syrphus valgus* Panzer.

Distribution : palaearctic 8 ; nearctic 4 ; oriental 1 ; holarctic 1.

*Xylotodes* Shannon, *Proc. U.S. Nat. Mus.* 69, No. 9, p. 22 (1926).

Resembles *Brachypalpus* with some smaller metallic species more like *Xylotomima*. Metasternum pilose. Scutellum with ventral fringe. First posterior cell petiolate. Subgenotype—*Brachypalpus inarmatus* Hunter.

Distribution : nearctic 8.

#### TEUCHOCNEMIS Osten-Sacken.

*Teuchocnemis* Osten-Sacken, *Bull. Buffalo Soc. Nat. Hist.* 2, 58-64 (1876).

Non-metallic, medium-sized species with rather wide, flattened abdomen, but little longer than wide. Face concave, lower part diagonal, subtruncate ; third antennal segment suborbicular. Metasternum pilose. Hind femora greatly thickened in males, less so in females ; male hind tibiae with short medial spur. First posterior cell petiolate ; third vein with moderate elongate curve. Genotype—*Pterallastes liturata* Osten-Sacken.

Distribution : nearctic 2.

#### KORINCHIA Edwards.

*Korinchia* Edwards, *J. F.M.S. Mus.* 8, 39 (1919).

Face deeply concave, the lower part of face and epistoma considerably produced diagonally forward, little or none downward. Fronto-antennal region protuberant, almost as much as epistoma. Antennae short ; third segment elongate oval ; eyes bare ; holoptic. Abdomen elongate oval, bluntly conical at apex. Hind femora slender, the basal setiferous patches not at all well developed and merging with the remainder of the pile. Hind tibiae slender. Loop of third vein deep but characteristic ; basal branch long and beginning at base of the anterior cross-vein. The distal branch more abrupt and vertical, the bottom of loop rather acute. Marginal cell petiolate or closed in the costa ; petiole of first posterior cell long or short. Antennal cross-vein oblique, entering fourth vein at distal fifth of discal cell. Genotype—*klossi* Edwards. While often regarded as a member of the *Eristalinae* I believe the absence of pile upon the metasternum and the almost complete or in

some cases complete absence of setae upon the hind femora necessitates the removal of *Korinchia* to the Xylotinae.

Distribution : palaearctic 3 ; oriental 9.

#### SYRITTOSYRPHUS Hull.

*Syrittosyrphus* Hull, *Ent. News*, 55, 203 (1944).

Rather large, short pilose species. Face slightly concave, diagonal and subtruncate below. Third antennal segment twice as long as wide. Eyes short, holoptic. Scutellum with deep rim and copious ventral fringe ; metasternum pilose posteriorly, this area separated by an oblique furrow or crease. Hind femora rather slender ; their coxae with long sharp spine ; coxae and all the sternites with long pile. First posterior cell without stalk ; third vein with deep oblique kink, the last section rectangular ; marginal cell widely open ; stigmal cross-vein present and a pre-apical wing fold present distal to the apical cross-vein. Anterior cross-vein oblique ; at distal third of discal cell. Petiole of anal cell very long as in *Milesia*, extending distalward beyond the lower angle of the discal cell. Related to *Korinchia*, the marginal cell open. Genotype—*opacea* Hull.

Distribution : Ethiopian (S. Africa) 1.

#### RHINOTROPIDIA Stackelberg.

*Rhinotropidia* Stackelberg, *Konowia*, 9, 224 (1930).

A remote genus. Face produced straight forward, immediately below the antennae into a long cone, broad at the base, rather pointed, the apex reaching just beyond the end of the short antennae ; segment about as long as wide. Hypopygium large and almost club-like. Hind femora strongly thickened and arched with subapically a strong tooth-like process beset with minute spines. Third vein deeply elongate concave ; anterior cross-vein entering fourth vein at distal third of discal cell. Apparently unique flies. Genotype—*Tropidia rostrata* Shiraki.

Distribution : palaearctic (Japan) 1.

#### PARATROPIDIA, new genus.

Flies of medium size, short to medium pilose, the abdomen tapering. Face long, the lower half greatly produced forward and downward, leaving the upper part concave ; face pubescent, pilose along eye margin ; no keels present. Scutellum or margin convex with ventral fringe ; metasternum pubescent. Hind femora considerably thickened, quite arched above, concave below ; subapically with a small setiferous tubercle ; the hind tibiae end transversely. First posterior cell without petiole ; anterior cross-vein oblique and beyond the outer third of the discal cell. Not very closely related to *Tropidia*, which the abdomen and perhaps the femora resemble ; perhaps closer to *Brachypalpus*. Genotype—*Tropidia bilineata* White.

Distribution : Australian 1.



## SYRITTA St. Fargeau and Serville.

*Syritta* St. Fargeau and Serville, *Encycl. Method.* **10**, 888 (1825).

This group contains small, pollinose-marked flies with slender, subcylindrical abdomen and massive, greatly thickened femora. Antennae short. Face concave and weakly carinate below, as in *Neplas*; without keel. Epistoma and lower face sometimes constricted and produced diagonally forward. Face short; eyes bare, exceedingly large. Scutellum without ventral fringe; metasternum pilose. Base of second abdominal segment laterally often with a vertical fan-like fringe of stout pile. Hind femora concave below with a long, apical, lateral, ventral, short spinose plate. First posterior cell with long petiole; third vein with elongate, rather deep concavity; last section of apical cross-vein rectangular. Genotype—*Musca pipiens* Linnaeus.

Distribution: palaearctic 4; nearctic 1; Ethiopian 21; oriental 6; Australian 1; Oceania 2; holarctic 1.

## NEPENTHOSYRPHUS de Meijere.

*Nepenthosyrphus* de Meijere, *Tijdschr. Ent.* **75**, 155 (1932).

A phylogeront. Remarkable flies, small, with short, cylindrical, reduced abdomen and enormously thickened and arched hind femora, which bear a long lateral plate which upon the outer half is beset medianly with a small tooth and outwardly with small spines. Eyes very large, pilose, narrowly holoptic; face quite convex. Antennae short, the third segment, however, about twice as long as wide. Metasternum pilose; scutellum with ventral fringe. Wing quite variable in the two species. In both, the anterior cross-vein is basal; at basal third in one and at basal fourth in the genotype. Marginal vein in genotype ending just past subcosta and before the small cross-vein; in the other much past the small cross-vein but not very near the submarginal vein. First posterior cell with a long petiole; both marginal cross-veins without spurs. Genotype—*tobaicus* de Meijere.

Distribution: oriental (Java) 2.

The author, while visiting the Zoological Museum at Amsterdam, illustrated the species. These remarkable flies were bred from water in the epiphytic pitcher plants of *Nepenthe*.

## SENOGASTER Macquart.

*Senogaster* Macquart, *Suite à Buffon*, **1**, 519–22 (1834).

*Acrochordonodes* Bigot, *Ann. Soc. ent. Fr.* (5), **8**, Bull. 97 (1878).

A remote genus. Elongate, slender flies; in the male the fourth segment and hypopygium are expanded into an oval elongated club; in the female the abdomen is less cylindrical, more flattened and the third and fourth segments each bear a pair of quite large, nodular bullae; base of abdomen wide. Head with the large eyes bare, the face small, short and deeply concave. Third antennal segment elongate. Scutellum with two or three hairs ventrally; metasternum pilose. Hind femora greatly thickened with a pair of large, lateral teeth subapically, the anterior one

Fig. 22.



## The Subfamily Xylotinae.

A. *Eriophora aureorufa* Philippi, dorsal view, hind femur, tibia; B. *Eriophora aureorufa* Philippi, antenna; C. *Eriophora aureorufa* Philippi, profile of head; D. *Macrometopia atra* Philippi, antenna; E. *Macrometopia atra* Philippi, hind femur and tibia (type); F. *Nepenthosyrphus tobaicus* de Meijere, dorsal view (type); G. *Nepenthosyrphus tobaicus* de Meijere, profile of head (type); H. *Nepenthosyrphus tobaicus* de Meijere, profile of head (type); I. *Macrometopia atra* Philippi, profile of head; J. *Nosodepus montensis* Hull, antenna (holotype).



Fig. 23.



## The Subfamily Xylotinae.

A. *Lycastria cornutus* Enderlein, dorsal view (type series); B. *Malometasternum tarsalis* Sack, profile of head; C. *Mutillomyia auricaudata* Williston, profile of head (type); D. *Mutillomyia auricaudata* Williston, antenna (type); E. *Malometasternum tarsalis* Sack, scutellum; F. *Syritosyrphus opacea* Hull, wing (holotype); G. *Pocota bomboides* Hunter, profile of head; H. *Mutillomyia auricaudata* Williston, hind femur, tibia (type); I. *Neplias* sp., profile of head; J. *Senogaster dentipes* Fabricius, dorsal view; K. *Senogaster dentipes* Fabricius, hind femur, tibia; L. *Senogaster dentipes* Fabricius, third femur, abdominal segments.

largest. First posterior cell with long stalk; venation much as in *Syritta*. Genotype—*Syrphus dentipes* Fabricius.

1. Distribution; neotropical (Brazil) 1.

#### TROPIDIA Meigen.

*Tropidia* Meigen, *Syst. Beschreibung*, 3, 346 (1822).

Not very large species. Often pollinose-marked. Abdomen tapered to the large hypopygium. Eyes bare. Face tricarinate, with sharp medial keel; straight or slightly arched. Antennae short. Scutellum with fringe; metasternum pilose. Hind femora greatly thickened, with prominent apical lateral plate. First posterior cell without petiole; third vein with elongate concavity. Genotype—*Musca scita* Harris.

Distribution: palaearctic 4; nearctic 8; neotropical 5; Ethiopian 1; Australian 1.

#### ORTHOLOPHUS Bigot.

*Ortholophus* Bigot, *Ann. ent. Soc. Fr.* (6), 2, Bull. 129 (1882).

Differing from *Tropidia*, especially in the fact that the vertically straight face, monocarinate but without prominent keels, juts out a considerable way immediately beneath the antennae. Genotype—*notatus* Bigot.

Distribution: neotropical (Chile) 1.

#### CERIOGASTER Williston.

*Ceriogaster* Williston, *Trans. Amer. Ent. Soc.* 15, 285 (1888).

A group of small flies, the narrow subcylindrical abdomen more or less constricted near the base. Eyes bare. Face concave; weakly carinate below. Third antennal segment elongate. Scutellum with sparse ventral fringe; metasternum pubescent. Hind femora greatly thickened. First posterior cell with petiole; venation much as in *Neplas*. Genotype—*foscithorax* Williston.

Distribution: neotropical 9.

#### TATUOMYIA Shannon.

*Tatuomyia* Shannon, *Proc. U.S. Nat. Mus.* 69, No. 9, p. 48 (1926).

A remote genus. Face tricarinate with three keels; third antennal segment elongate, eyes holoptic and bare. Metasternum pubescent. Abdomen strongly constricted and petiolate, the distal expansion beginning close to the end of the elongate second segment, remainder club-like. Hind femora very greatly thickened with spines below, their tibiae bidentate apically. First posterior cell with petiole. Genotype—*batesi* Shannon.

Distribution: neotropical 1.

Recognized subgenera: *Senoceria* Hull, *Trans. Amer. Ent. Soc.* 56, 146 (1930).

Similar to *Tatuomyia*; very short pilose, nearly bare flies. Abdomen constricted but without long slender, subcylindrical petiole; expansion of distal part begins near base of second segment. Scutellum with ventral fringe, metasternum pubescent.



Hind femora greatly thickened with long spines below and a subbasal claw-like series; hind tibiae with one spur. First posterior cell with a long petiole; third vein with very slight curvature; anterior cross-vein just past middle of discal cell. Genotype—*Xylota coarctata* Wiedemann (*spiniformorata* Hull).

Distribution: neotropical 1.

#### CREPIDOMYIA Shannon.

*Crepidomyia* Shannon, *Proc. U.S. Nat. Mus.* **69**, No. 9, p. 47 (1926).

Medium-sized, dark, bare, short pilose flies. Face tricarinate, with three keels. Eyes bare and holoptic. Third antennal segment elongate. Scutellum with ventral fringe; metasternum pubescent. Abdomen flattened, elongate, yet not narrow and with scarcely any trace of narrowing basally. Hind femora considerably thickened especially in the middle, and with long spines beneath; tibiae shortened, arcuate, with one spur. Venation rather similar to *Tatuomyia*. Genotype—*tricrepis* Shannon.

Distribution: neotropical 3; oriental 1 (probably belongs elsewhere).

#### MALOMETASTERNUM Shannon.

*Malometasternum* Shannon, *Proc. ent. Soc. Wash.* **29**, 86 (1927).

Short and broad; eyes bare and holoptic. Face dropping vertically beneath antennae, then produced forward into a conspicuous tubercle near the middle; the face continues to descend below the tubercle, the lower part of the face rather deeply produced. Scutellum wide, transverse, rounded at corners, without rim and with a prominent tubercle on either side; metasternum pilose. Abdomen only a little elongate. Hind femora greatly thickened, especially on basal half, and with subapical lateral, non-spinose plate. First posterior cell with short petiole; anterior cross-vein quite oblique, entering fourth vein at discal third. Genotype—*scutellaris* Shannon.

Distribution: Australian 1.

#### CALLIPROBOLA Rondani.

*Calliprobola* Rondani, *Dipt. Ital. Prodr.* **1**, 204 (1856).

Large, short pilose, bright metallic aeneous or cupreous flies. Eyes bare and holoptic. Front and upper face produced out in a large conspicuous cone. Third antennal segment deeper than long. Scutellum with ventral fringe; metasternum pubescent. Abdomen with rather heavy mats of appressed pile bordering the posterior margins of the segments. Hind femora rather slender and but slightly thickened. Venation much as in *Xylota*; first posterior cell petiolate. Genotype—*Syrphus speciosa* Rossi.

Distribution: palaearctic 4.

#### CHRYSOSOMIDIA Curran.

*Chrysosomidia* Curran, *N. Amer. Dipt.* 271 (1934).

Apparently the only difference in these flies from *Xylota*, apart from the greater size and more brassy colour, is the matted pile bordering the segments; these are

weak distinctions. Related to *Calliprobola* which, however, has quite conical, produced front and facial region and third antennal segment deeper than long. Genotype—*Calliprobola crawfordi* Shannon.

Distribution : nearctic 5.

#### CYNORHINA Williston.

*Cynorhina* Williston, *Bull U.S. Nat. Mus.* **31**, 209 (1886).

Medium-sized to small flies. Face concave below antennae, then produced somewhat; face often slightly concave upon the upper half or slightly convex or with a weak tubercle near the middle which may be merged with the slightly more produced lower face. Third antennal segment approximately suborbicular; sometimes a little deeper than long. Front not greatly produced. Eyes bare and holoptic, sometimes narrowly. Metasternum pubescent. First posterior cell either petiolate or non-petiolate. Hind femora either slender or rather considerably thickened. A variable genus; a few species resemble *Criorrhina* but the metasternum is pubescent. Genotype—*Milesia analis* Macquart.

Distribution : palaearctic 4; nearctic 17; -oriental 3.

Recognized subgenera : *Somula* Macquart, *Dipt. Exot. suppl.* 2 (1847).

Related to *Cynorhina*. Front and antennal region greatly produced into a pedicel which bears the short antennae; third antennal segment orbicular. Eyes bare, dichoptic. Face nearly vertical in profile, barely concave above, barely convex below. Scutellum without fringe; metasternum pubescent. Abdomen oval. Hind femora slender. Venation as in *Cynorhina*, the first posterior cell without petiole. Large flies with yellow face and abdomen brightly marked with yellow. Genotype—*decora* Macquart.

Distribution : nearctic 2.

#### STERPHUS Philippi.

*Sterphus* Philippi, *Verh. Zool-bot. Ges. Wien*, **15**, 737 (1865).

Face retreating and slightly concave between the antennae and the lower half of face which is slightly convex; epistoma not produced; third antennal segment longest below and scarcely as long as wide. Eyes bare and holoptic. Face uniformly thickly pubescent and without pile except upon the antennocular line. Scutellum with fringe; metasternum pubescent. Hind femora simple. Venation much as in *Xylota*. First posterior cell with long petiole. Large, elongate flies. Genotype—*Xylota coerulea* Rondani.

Distribution : neotropical (Chile) 2.

#### STILBOSOMA Philippi.

*Stilbosoma* Philippi, *Verh. Zool-bot. Ges. Wien*, **15**, 736 (1865).

A remote genus. Upper face and front produced forward into a large, elongate cone with broad base which bears the antennae. Face deeply concave; the epistoma produced only a little way and not as far as the front; eyes of male dichoptic. Antennae short; third segment suborbicular, barely deeper than long.



Scutellum with fringe; metasternum pilose. Abdomen very broad, short, rather flattened and wider than thorax. Hind femora a little thickened throughout and bearing subapically a prominent, lateral double tooth, the anterior one the largest. Wings dark; first posterior cell without petiole; anterior cross-vein remarkably long and oblique, bearing on its distal recurved fifth a long, free-ending, distal spur. This spur may quite probably be remains of the fifth radius. The last section of the cross-vein enters the fourth vein at its distal fourth. Genotype—*rubiceps* Philippi.

Distribution: neotropical (Chile) 2.

#### MILESIA Latreille.

*Milesia* Latreille, *Hist. Nat. Crust. Insect.* 14, 361 (1804).

Face large or well developed in profile; usually nearly straight or slightly concave above; face prominent upon lower half but never greatly produced downward. Antennae short, the third segment orbicular, or a little deeper than long. Eyes bare, usually holoptic, sometimes narrowly dichoptic. Scutellum with fringe; metasternum pilose. Abdomen elongate but as a rule not very narrow. Hind femora elongate and stout without being noticeably thickened; the femora frequently bear a small, subapical, dentate projection. Wing venation characteristic; first posterior cell with or without petiole; marginal cell closed; anterior cross-vein very oblique, entering fourth vein at last sixth of discal cell; petiole of anal cell very long, paralleling wing margin. Very large handsome flies. Genotype—*Musca semiluctifera* Villeneuve.

Distribution: palaearctic 7; nearctic 5; neotropical 2; oriental 36.

#### POGONOSYRPHUS Malloch.

*Pogonosyrphus* Malloch, *Stylops*, 1, 125 (1932).

Very large flies, similar to and related to *Milesia*, with the marginal cell open. Face large, greatly produced forward throughout and upon the lower part also produced downward to some extent. Profile nearly straight and very slightly concave. Antennae a little elongated; third segment nearly twice as long as wide. Third vein with a slight angular dip bearing an oblique, short, distalward spur; anterior cross-vein as in *Milesia*; lower marginal and apical cross-veins meet practically without bend or interruptions as in *Deineches*; petiole of anal cell short and recurved. Genotype—*arnoldi* Malloch.

Distribution: Ethiopian (S. Africa) 1.

#### SPILOMYIA Meigen.

*Spilomyia* Meigen, In *Illiger Mag. f. Insektenkunde*, 2, 273 (1803).

Face nearly straight in profile, minutely produced at the epistoma or with a minute tubercle in the middle. Antennae with first and second segments elongate; third orbicular; antennae shortest in the genotype and its European relatives, longest in nearctic species. Eyes bare and marked with irregular vertical stripes or bands of spots. Scutellum with or without fringe; metasternum pilose, with a blunt angular tubercle in front. Abdomen large, convex, subcylindrical and elongate. Hind femora simple, with a prominent subapical dentate spur. Vena-

tion as in *Milesia* except that the marginal cell is widely open; anterior wing margin brown. First posterior cell without petiole. Large, bright coloured wasp-mimics. Genotype—*Syrphus saltuum* Fabricius.

Distribution: palaearctic 8; nearctic 9; neotropical 5.

I place *Spilomyia* in Milesini on the basis of the similarity in its wings and femora.

#### TEMNOSTOMA St. Fargeau and Serville.

*Temnostoma* St. Fargeau and Serville, *Encycl. Method.* 10, 518 (1825).

Face concave in the females, in the males often with a weak tubercle. Antennae short, the third segment nearly or quite orbicular. Eyes bare and usually holoptic; sometimes narrowly dichoptic. Scutellum with fringe; metasternum pilose, tending to become pubescent in a few species which have only a very few hairs. Abdomen elongate, becoming more slender in the smaller species. Hind femora simple. First posterior cell of wing without petiole; cross-vein entering fourth vein at or very close to the middle of the discal cell. Large to small, wasp-like flies. Characteristically marked with yellow or grey pollen. Genotype—*Milesia bombylans* Fabricius.

Distribution: palaearctic 10; nearctic 11; oriental 2; holartic 1.

The smaller species meet most of the requirements of a generalized member of the Xylotinae, excepting perhaps the bareness and pollinose markings; some of the smaller species are not greatly different from *Myiolepta*.

#### SPHECOMYIA Latreille.

*Sphecomyia* Latreille, *Cuvier Règne Anim.* ed. 2, 5, 495 (1829).

Face well developed. Upon the lower half and greatly produced downward; concave either slightly or much upon the upper part. Eyes bare and narrowly dichoptic in some males. First and second segments of antennae usually elongate, often greatly so; third usually orbicular. Scutellum with fringe; metasternum pilose. Abdomen large, elongate, convex. Hind femora simple. Venation similar to *Temnostoma*, the first posterior cell with or without petiole, the cross-vein a little beyond middle of discal cell. Large, handsome, yellow pollinose, wasp-mimics. Genotype—*Chrysotoxum vittatum* Wiedemann.

Distribution: palaearctic 1; nearctic 5; holartic 1.

#### CACOCERIA Hull.\*

*Cacomyia* Hull, *Trans. Amer. Ent. Soc.* 56, 146 (1930); preoccupied.

*Cacoceria* Hull, *Ent. News*, 47, 227 (1936).

A remote genus. Face pubescent but produced below, nearly straight in profile with a small tubercle in the middle; first and second segments of antennae slender and quite elongate; third broken off beyond the dorsal arista (in each specimen of both of the only two known species); eyes bare. Scutellum with fringe. Metasternum pubescent. Abdomen elongate and greatly constricted upon the second

\* In 1930 the author described *Cacoceria* (as *Cacomyia*) from a Mexican species based upon a single female in which the greater part of the third antennal segment was missing. He has recently received a pair of specimens of an undescribed species of this genus from Peru. The male has a deeply fissicorn third antennal segment, the two prongs of equal length, long and slender and adjacent. Including *Masarygus* Brethes and *Cervicorniphora* Hull, this is the third fissicorn genus of Syrphid flies.



segment. Hind femora very greatly enlarged except upon the spindly basal sixth, the apex also narrowed ; with several long, apical, spinous chaetae below. Anterior cross-vein enters discal cell just before the middle ; first posterior cell with long petiole. Genotype—*Cacomylia cressoni* Hull.

Distribution : neotropical 1 (and one undescribed).

#### MUTILLIMYIA Hull.

*Mutillimylia* Hull, *Rev. Soc. Ent. Argent.* **12**, 139 (1943).

Face slightly retreating, subcarinate, elongate-convex in the middle, sides pubescent striped ; antennae moderately elongate on all segments and pubescent, third segment longest below, subtruncate. Eyes bare, barely touching in male. Scutellum with ventral fringe ; metasternum pubescent. Abdomen elongate, greatly constricted upon the second segment which is of medium length ; remaining segments with thick, flat appressed golden pile, projecting beyond each segment. Hind femora simple, without spines. Venation much as in *Temnostoma*. Genotype—*Ceriogaster auricaudata* Williston.

Distribution : neotropical (Mexico) 1.

#### CRIORRHINA Meigen.

*Criorrhina* Meigen, *Syst. Beschreibung*, **3**, 326 (1822).

Face concave upon upper half, produced chiefly forward below with or without a small tubercle that may be merged with the lower part of face. Sides of face long pilose, sometimes with mystax above epistoma. Antennae short ; third segment decidedly deeper than longer, the rounded apex bearing the subbasal arista. Eyes bare, narrowly dichoptic in at least some males. Metasternum pilose. Abdomen from wide to short oval. Hind femora from slender to greatly thickened. First posterior cell usually with a long petiole, sometimes without ; anterior cross-vein enters the fourth vein from the last one-fourth to the last one-fifth of the discal cell. These are medium or large flies, characteristically long pilose and woolly. Bumblebee-like. Genotype—*Syrphus asilica* Fallen.

Distribution : palaearctic 7 ; nearctic 16 ; neotropical 3 ; oriental 19 ; Australian. 6

#### ERIPHORA Philippi.

*Eriophora* Philippi, *Verh. Zool-bot. Ges. Wien*, **15**, 735 (1865).

Very similar to *Criorrhina* in most respects. Face slightly concave above. Third antennal segment nearly orbicular, longest below. Eyes bare, narrowly touching in male. Metasternum pilose. Abdomen wide and short, a little more elongate in male. Hind femora slightly enlarged in the middle. First posterior cell with a long stalk. These are quite large, reddish-orange coloured, reddish orange pilose, shorter pilose flies. Genotype—*aureorufa* Philippi.

Distribution : neotropical (Chile) 1.

There is a parallelism between these pale Criorrhinini in their relation to the dark coloured remainder of the genus and the orange coloured Chilean species of *Cheilosia*.

## MERAPIOIDUS Bigot.

*Merapioidus* Bigot, *Ann. Soc. Ent. Fr.* (5), **9** (1879).

A remote genus. Face nearly straight with a well-developed tubercle in the middle. Eyes bare, widely dichoptic. Third antennal segment very deep, pyriform, the dorsal attenuated peak bearing the arista. Metasternum pilose. Abdomen large, oval. Hind femora slender. First posterior cell with long petiole. Large and long pilose, especially on head and thorax. Genotype—*villosus* Bigot.

Distribution : nearctic 1.

## DEINECHES Walker.

*Deineches* Walker, *Insecta Saundersiana Dipt.* **1**, 227 (1852).

Face without pile, concave above, greatly produced downward below. Antennae short. Eyes bare and holoptic. Scutellum with ventral fringe; metasternum pilose; abdomen elongate but not narrow, flattened basally and slightly tapering apically. Hind femora much thickened throughout with short obtuse, apical, lateral spur. First posterior cell much attenuated apically without petiole; anterior cross-vein enters fourth vein between distal fourth to fifth of discal cell. Large dense, short pilose flies. Genotype—*nigrofulva* Walker.

Distribution : Australian 1.

## NOSODEPUS Speiser.

*Nosodepus* Speiser, *Jb. Nassau ver. Naturk.* **66**, 131 (1914).

Face deeply produced, straight in profile except for large middle tubercle. Face vittate pubescent without pile, except on stripes and opposite antennae. Antennae a little elongate upon first and more upon second segment; third obliquely subtruncate, longest below. Eyes pilose. Abdomen large, short, subcircular, wider than thorax. Hind femora slender. First posterior cell with short petiole; anterior cross-vein at distal fourth of discal cell. Large, long pilose, montane flies. Genotype—*minotaurus* Speiser.

Distribution : neotropical (Peru, Venezuela) 2.

## MACROMETOPIA Philippi.

*Macrometopia* Philippi, *Verh. Zool-bot. Ges. Wien*, **15**, 740 (1865).

Front produced; face slightly retreating, rather deep below, with low tubercle in the middle; face long pilose on sides. Antennae deeper than long, longest below. Eyes dense and long pilose, narrowly holoptic. Metasternum pubescent. Abdomen elongate oval. Hind femora slender, long pilose. First posterior cell attenuated, without petiole; anterior cross-vein just past middle of discal cell; wing slender; petiole of anal cell parallel and evanescent. Long pilose flies. Genotype—*atra* Philippi.

Distribution : neotropical (Chile) 1.



## CRIOPRORA Osten-Sacken.

*Crioprora* Osten-Sacken, *Cat. Dipt. N. Amer.* 2, 136, 251 (1878).

Face concave and narrowly produced diagonally downward below and laterally compressed or pinched together. Antennae short. Eyes bare and narrowly holoptic or narrowly dichoptic. Metasternum pubescent. Abdomen elongate-oval. Hind femora greatly thickened, somewhat shortened and arcuate. First posterior cell with long stalk; anterior cross-vein enters fourth vein a little past middle of discal cell. Large, long pilose flies. Genotype—*alopez* Osten-Sacken.

Distribution: nearctic 4; neotropical 2.

## PHILIPPIMYIA Shannon.

*Philippimyia* Shannon, *Proc. U.S. Nat. Mus.* 69, No. 9, p. 47 (1926).

Face receding; concave; a little produced at epistoma. Face non-pubescent, with no pile except on the stripes. Antennae short. Eyes bare. Scutellum with fringe; metasternum pubescent. Abdomen short oval; convex. Hind femora simple. First posterior cell virtually without petiole; third vein elongate-concave; anterior cross-vein enters fourth vein just past middle of discal cell. Rather large, metallic flies with blackish wings. Genotype—*Sterphus cyanocephala* Philippi.

Distribution: neotropical (Chile) 1.

## POCOTA St. Fargeau and Serville.

*Pocota* St. Fargeau and Serville, *Encycl. Method.* 10, 518 (1825).

Head small, face concave, epistoma produced. Face pubescent, without pile except on the stripes. Antennae short, third segment deeper than long. Eyes bare, holoptic. Scutellum with fringe; metasternum pubescent. Abdomen large, convex, wide as thorax; but little tapering. Hind femora simple. First posterior cell apetiolate; third vein very shallowly concave; anterior cross-vein ends before distal third of discal cell. Large, short, dense pilose, bumblebee-like flies. Genotype—*Musca apiformis* Schrank.

## HADROMYIA Williston.

*Hadromyia* Williston, *Canad. Ent.* 14, 79 (1882).

Similar to *Pocota* but very large flies; the first posterior cell with a long petiole; middle femora of male at base with very long, thick, curved spur. Metasternum pubescent. Bumblebee-like. Genotype—*grandis* Williston.

Distribution: nearctic 1.

## LYCASTRIS Walker.

*Lycastris* Walker, *Trans. Ent. Soc. Lond.* N.S. 4, 155 (1857).

A phylogeront. Face produced into a slender, conical, porrect snout far beyond antennae; proboscis slender and still longer. Antennae short; third segment a little elongate and conically pointed. Eyes bare. Metasternum pubescent. Abdomen quite wide and short, slightly convex, apt to be recurved downward in female. Hind femora slender. First posterior cell apetiolate; third vein nearly straight; marginal cell with numerous extra cross-veins; anterior cross-vein enters fourth vein almost at apex of discal cell. Large, rather long, dense pilose flies. Genotype—*albipes* Walker.

Distribution: oriental 4.

## PTERALLASTES Loew.

*Pterallastes* Loew, *Centuries*, 9, 80 (1863).

Face concave, the lower face short and the epistoma not protuding; eyes bare and holoptic; antennae short and oval. These are short but thick pilose flies with unicolorous thorax; the metasternum is pilose, the scutellum with copious fringe. Abdomen oval, as wide as thorax. Hind femora stout without being thickened; there are no differentiated setae at the base of the hind pair. Third longitudinal vein with a pronounced dip, the first posterior cell with a short petiole; stigmal cross-vein present; the oblique anterior cross-vein lies two-thirds of the distance from the base of the discal cell; marginal cell open; sixth vein nearly straight.

Genotype—*thoracicus* Loew.

Distribution: nearctic 1.

## HEMIXYLOTA Shannon and Aubertin.\*

*Hemixylota* Shannon and Aubertin, *Dipt. Patagon. S. Chile*, 6, 146 (1933).

Face deeply concave, the epistoma protuding in consequence, but the lower face quite short, and transverse below. Antennae large, deeper than long, suborbicular; front prominent and the eyes bare and dichoptic in males; metasternum pubescent only, the scutellum with impressed rim and ventral fringe. Abdomen elongate; not quite so wide as thorax. Hind femora slender without differentiated setae basally, though such patches are present on the first four. Third vein straight; marginal cell widely open; whole stigma dark, without cross-vein; anterior cross-vein nearly transverse and lying well before the middle of the discal cell; first posterior cell with a rather long petiole; shining, short pilose flies. Genotype—*varipes* Shannon and Aubertin.

This fly appears to be an aberrant member of the Xylotinae; the slender femora, the basal anterior cross-vein and dichoptic eyes indicate that it is a quite generalized type.

Distribution: neotropical (Chile) 1.

*Xylotosyrphus* Hull (fossil genus). Characterized by: being *Xylota*-like even to the tetramaculate slender abdomen, but the anterior cross-vein is well before the middle of discal cell; hind femora enlarged. Genotype—*pulchrafenestra* Hull.

*Megaxylota* Hull (fossil genus). Characterized by: hind femora greatly thickened, without spines; *Xylota*-like; abdomen twice as long as wide; face concave. Genotype—*magnifemur* Hull.

## HARDIMYIA Ferguson.

*Hardimyia* Ferguson, *Proc. Linn. Soc. N.S.W.* 51, 533 (1926); Hardy, *Australian Zoologist*, 2, 13 (*Chrysotoxum elongatum*), figs. 1-2 (1921).

A rather small fly with bare eyes which are contiguous in the male for a short distance; upper anterior facets a little larger than the others; eyes of female

\* *Eoxylota* Hull (1945), p. 324. Related to *Hemixylota* from which it is distinguished by the less sigmoid apical cross-vein and by the impressed scutellum. Originally placed by me in the Cheilosinae on account of the basal position of the small cross-vein, I have now relegated it, together with *Hemixylota*, to the Xylotinae. Genotype—*Xylota pulchra* Meunier.



widely separated. The head is quite short but wide and high, perhaps even wider than the thorax. The front is a little produced and the face, which is nearly straight in profile, has a very slight, short concavity opposite the bottom of the eyes, is rather deeply produced downward below. The antennae are quite elongate, the last two segments subequal, the middle one longest, and the third segment about twice the length of the first ; the antennae are somewhat porrect, the arista dorsal and basal. The thorax is oblongate. The abdomen is elongate, slightly narrowed as far as the end of the second segment, upon which it is flattened above ; remaining two segments subcylindrical ; the first segment is rather long, extending beyond the scutellum. The hind femora are rather strongly thickened in the middle and their tibiae bowed. Upon the wing the third vein ends but a short distance beyond the costa, the marginal cell hence very widely open. The third vein ends at or very near the apex, its confluence with the subapical cross-vein however is some distance back ; the latter is sinuous and oblique, long and parallels the wing margin. The anterior cross-vein is quite oblique but lies at the middle of the discal cell. The alula is well developed, the sixth vein arched posteriorly ; vena spuria present.

The description I give is partly taken from that of Ferguson and the two illustrations by Hardy. Ferguson is quite right in removing this fly from the Chrysotoxinae ; he suggested a relationship with *Xylota*. This is probably the correct assignment, but it is possible that the elongate, porrect antennae, general form of the abdomen and position of the small cross-vein ally it to *Psarus*. I place the genus tentatively here until such time as it can be studied more fully. Like so many *Xylota* species there are a pair of conspicuous yellow spots upon the second segment.

#### THE SUBFAMILY PSARINAE.

I place here an isolated European genus that stands out to some extent from the Cheilosinae, to which it is perhaps closest related. The antennal process and antennae might suggest *Chrysotoxum*, were not the abdomen and the pilose humeri definitely contrary to this view. There are no other Cheilosinae that approach it at all. Nevertheless, it would be worth recalling that in the Xylotinae such a type of frontal antennal process is not uncommon (*Somula*, *Spilomyia* and perhaps others) and the true affinity of *Psarus* may be here. In *Somula* the small cross-vein is not much farther placed distally than it is in *Psarus*, although it is true that it is beyond the middle.

#### PSARUS Latreille.

*Psarus* Latreille, *Hist. Nat. Crust. Insect.* 14, 357 (1804).

The head is broadly oval in profile and not especially short. The eyes are dichoptic in the male. The vertex is a little swollen, the post-occiput above tumid, but narrowly so ; the front less than one-half as wide as the vertex at the top. The ocelli are widely spaced in a triangle. The front is carried out into a long and conspicuous process. The antennae are elongate, and all the segments partake of the elongation ; second segment two and one-fourth times as long as the first ; the third segment is a little shorter than the second. The arista is shorter than the third segment, grotesquely thickened, pubescent and pallid. Below the antennal

prominence the face quickly retreats to a point a little above the bottom of the eyes, where it begins to slope forward to a long, low, obtuse tubercle, just opposite to the bottom of the eyes, then descending quickly and dropping a very short distance to the edge of the epistoma. The face is thus bluntly and conically produced and is bare of pile except above the mouth border, but is pubescent along the sides. The occiput is not visible in profile, except for a short distance above. The thorax is narrower than the head, elongate, beset with short, appressed, stubby hair on the dorsum, the thin, elongate, semicircular scutellum and the pleura. The abdomen a little more than twice as long as wide, with practically parallel sides which are strongly rounded and turned over, although the disc is practically flat, except on the last segment which is quite convex. Abdomen composed of four visible segments, the last three nearly equal in length, the fourth a little the longest. The hind femora and tibiae quite slender, the latter a little shorter than the femora; hind femora basally beset with a few short, stiff bristles, but no spines. The hind tibiae has a spinose bristly ending. The wings are short and broad, barely longer than the abdomen. The subapical and postical cross-veins nearly parallel the wing margin; the former, however, is recurrent and joins the third vein some distance back of the apex, which together with the costa ends at apex of wing. The fourth longitudinal vein curves down sharply to meet the postical cross-vein. First posterior cell with a rounded angle, the second posterior cell with a well-developed spur; submarginal cell widely open; no stigmal cross-vein; vena spuria faint. Genotype—*Syrphus abdominalis* Fabricius.

Distribution: palaearctic (Europe) 1. A highly aberrant, small fly reported to have a peculiar affinity for wild geraniums.

#### THE SUBFAMILY CERIOIDINAE.

These are beautiful, bright coloured, wasp-like flies of striking aspect, ranging from medium to large size. All are elongate, with elongate antennae, but the abdomen varies from very slender and petiolate, thread-waisted types with bulbous apex, down to relatively short subcylindrical types with rather wide abdomen. A further outstanding characteristic is the bare, even scrobiculate aspect, for the pile has been reduced to thick pubescence or to microsetae. The legs are rather simple, the hind femora usually showing but little thickening. The wings are pointed at apex, narrow and elongate and the venation is rather characteristic. The third vein, which often has a pronounced loop with or without an appendix vein, is joined by the apical cross-vein quite at the apex of the wing. The anterior cross-vein, always beyond the middle of the discal cell, is often very close to the end of that cell. There is usually a stigmatic vein. These flies are widely distributed, and are found in all the principal world regions including oceania. They are more abundant in the tropical regions and are essentially tropicopolitan.

The relationship of these flies to other subfamilies presents difficult problems that are not easily solved. They are among the most highly modified members of the family and have specialized to a remarkable extent along mimetic lines. While there is some reason to believe that this subfamily is young in point of development, and has recently evolved, yet there is comparatively little clue, except what may be



possibly afforded by *Psarus*, to their origin, which may have been a long time back. *Psarus* reminds us of Cerioidinae in several ways. These flies are relatively bare, short, setate pilose, with an abdomen not unlike *Tenthredomyia*. The frontal antennifer is well developed, and upon the elongate antennae the thickened, shortened, three-segmented arista has moved so far toward the apex of the segment that it is beyond the middle. Lastly the wing is not greatly like *Cerioides*, but it would only have to be lengthened, and the ending of the apical cross-vein changed to convert it. To this author it seems not unlikely that *Psarus* is its nearest living relative. This concept of the subfamily would derive them from the ancestral Syrphinae at an early time. Another view is possible; the venation of the subfamily is very close to that of many Xylotinae, the stigmatic cross-vein and the occasional appendix excepted, and the possible relationship to the Xylotinae, where petiolate types have arisen, cannot be overlooked. No fossil species are known, but it must be remembered that the individuals of this family are scarce indeed in temperate zones, whence come most of our fossil-yielding beds.

The facies of this subfamily are so uniform that no tribes are here recognized. Two groups may be noticed upon the basis of the condition of the antennifer. It is possible in one group, that some of the more filiform types have reached the approximate end of their development and might be regarded as phylogeronts. In one group the antennifer has never developed, or if it has, it has receded in the course of time; in this group the antennal segments are more elongate, whereas in those in which the antennifer itself is especially long, the segments themselves may be quite short. Thus, the net extent of lengthening tends to remain about the same. The length of the antennifer does, however, vary considerably, and one of the trends of the subfamily might be considered to be such elongations. Yet we must still account for those species with a long antennifer and exceptionally short antennae. This would seem to indicate that the antennifer has lengthened independently of the antennae.

All the genera have the antennae styloform, the third segment with a three-segmented style. The tumid occiput, especially behind the ocelli, is characteristic. Males holoptic in all genera. The anterior margin of the wing is dark brown in all species known to me, and the wing is often folded back along the line of the cubital vein, thus further simulating the wing of wasps.

*A key to the groups of the subfamily Cerioidinae.*

1. Frontal process upon which the antennae are fixed greatly produced, longer than the length of the first joint of the antennae. Male hypopygium often globose. The metasternum behind is membranous. Semblance of a stigmatic cross-vein present ..... 2  
Antennifer much reduced to absent altogether. As a general rule not over half-length of the first joint. Stigmatic cross-vein absent. Abdomen not always constricted basally. Male hypopygium tending to be pointed but exceptions occur ..... 3
2. Abdomen thick at base; but little constricted. Anterior abdominal corners bright yellow. Loop of third vein spurred. (Including *Pterygophoromyia* subgenus) ..... *Tenthredomyia* Shannon.
- Abdomen obviously basally petiolate and constricted. Anterior corners dark. Third vein seldom spurred ..... *Monoceromyia* Shannon.

3. Abdomen not constricted basally ..... *Primocerioides* Shannon.  
 Abdomen at least slightly constricted at the base ; usually strongly  
 constricted ..... 4
4. Metasternum completely chitin-circled ..... 5  
 Metasternum membranous posteriorly ..... *Cerioides* Rondani.
5. Abdomen but little narrowed basally ; some three or four times as  
 thick at the end as at the beginning of the second segment.  
 Abdominal elongation shared by all the segments. Abdomen  
 pointed at tip. Mimicking the polistine wasps ..... *Polistoceria*, subgen. n.  
 Abdomen gracefully slender at waist ; quite narrow ..... 6
6. Second segment about as wide at apex as at base ; five to eight times  
 as long as wide (laterally). Abdominal tip bulbous, not pointed. *Ceriathrix*, subgen. n.  
 Second segment wider at end than at base ; only about four times as  
 long as wide or less. Abdomen pointed at tip. Mimicking the  
*Polybia* group of wasps ..... *Polybiomyia* Shannon.

## PRIMOCERIOIDES Shannon.

*Primocerioides* Shannon, *J. Wash. Acad. Sci.* **17**, 41 (1927).

The non-constricted abdomen and the absence of the antennifer mark this group as the most generalized genus in the subfamily.

The genotype is peculiar in several particulars. The pubescence is unusually well developed, the eyes and face are distinctly pilose ; the first antennal segment is long, the second short, and the third fairly long. The third longitudinal vein is straight and bears a spur vein projecting into the first posterior cell. Genotype—*Cerioides petri* Hervé-Bazin.

Distribution : oriental (Japan) 1.

## TENTHREDOMYIA Shannon.

*Tenthredomyia* Shannon, *Insec. Inscit. Mens.* **13**, 50 (1925).

*Sphyximorphoides* Shiraki, *Mem. Fac. Sci. Agric. Taihoku*, **1**, 6 (1930).

Elongate, small to medium-sized flies with bright yellow and black markings. The occiput is extravagantly developed above and below and least developed where the occiput fits tightly over the humeri. Cheeks thick but not prominent. Face well developed ventrally ; more or less straight in profile. Antennifer quite long. Scutellum short, without ventral fringe. Metanotum relatively inconspicuous. Metasternum and humeri pilose. Abdomen scarcely constricted at base, with bright markings in the anterior corners. Hypopygium more or less rounded in the male. Hind femora slightly thickened ; equipped with a ventral row of spines on either side and often for greater part of length of the femora ; hind tibiae thicker apically. Loop of third vein with a spur ; apical cross-vein, third vein and costa end at tip of wing. Genotype—*Ceria abbreviata* Loew.

Distribution : palaearctic 5 ; nearctic 7 ; Ethiopian 1 ; oriental 9 ; Australian 9.

Recognized subgenera : *Pterygophoromyia* Shannon, *J. Wash. Acad. Sci.* **17**, 42 (1927).

*Cerioides*-like flies characterized by the presence of a small but distinct plumula. Subgenotype—*Tenthredomyia saundersi* Shannon.

Distribution : Australian 1.



## CERIOIDES Rondani.

*Cerioides* Rondani, *Ann. Ent. Soc. Fr.* (2), **8**, 211 (1850).

*Styloceria* Enderlein, *Tierwelt Mitteil Europa*, **6**, 3, Teil 2, Lief. 16 (1936).

Elongate, large flies with often bright yellow markings on a black background. Upper occiput tumid. Face projecting downwards, usually nearly straight in profile and retreating above the epistoma; cheeks well developed. Antennifer poorly developed to practically absent. Antennae stylete, the first segment a little longer than the second, the last two subequal, and the third basally thickened; the second segment is apically thickened so that the two last segments appear as one body; third segment with an apical style which is often pale. Scutellum short; abdomen but little constricted at base; in the genotype the greatest constriction lies just past the base of the second segment. Abdomen elongate, very convex, subcylindrical. Femora considerably thickened, as far as members of this subfamily are concerned, two or three times as wide in the middle as at the ends; the hind femora ventrally with stout setigerous bristles. Fore border of wings brownish. In the genotype there is an adventitious branch to the third vein but almost no dip. Apical cross-vein, third vein and costa end at tip of wing; posterior margin somewhat chitinized. Genotype—*Sphyximorpha subsessilis* Rondani.

Distribution: palaearctic 8; nearctic 7; neotropical 28; Ethiopian 13; oriental 11; Australian 3; Oceania 2.

## POLYBIOMYIA Shannon.

*Polybiomyia* Shannon, *Insec. Inscit. Mens.* **13**, 56 (1925).

The antennifer is like that of *Cerioides*, very small, much shorter than the length of the first antennal joint. Face projecting below. Metasternum apically circled completely by chitin, a condition which varies in some species. Scutellum is quite short; metanotum conspicuous. Humeri pilose; metasternum more or less pilose or pubescent. Abdomen pointed at tip. Hind femora slightly thickened, bearing short teeth ventrally and apically. Apical cross-vein and third vein end together with the costa shortly before the tip of the wing; third vein appendiculate. Genotype—*schwarzi* Shannon.

Distribution: nearctic 6; neotropical 10; Ethiopian 1; oriental 1.

Recognized subgenera: *Polistoceria*, new subgenus.

The subgenus differs from *Polybiomyia* in the short petiolate abdomen; the club-shaped part is gradually drawn out and not short and bulbous as in *Polybiomyia*.

Abdomen narrowest at extreme base of second segment, the apex of this segment is four or five times as wide as its width basally. The remaining segments are elongate, the tip of the abdomen pointed, the contraction of the abdomen uniformly spread out over all the segments. Hind femora considerably thickened, especially thickened basally; hind tibiae ending sharply. The third vein is nearly straight with a well-developed adventitious vein. The apical cross-vein joins the third vein near the apex of the wing. The genotype—*Cerioides kerteszi* Shannon.

Distribution: neotropical 4.

This species, *kerteszi*, together perhaps with *facialis*, *braueri*, *roederi*, seem to form a natural group of *Polistes*-mimicking flies.

*Ceriathrix*, new subgenus.

A phylogeront. Antennifer quite short. Second and third antennal segments are subequal; third quite short; the second, therefore, long and tapering. Basal segments of abdomen very long and slender, pipe-like, seven or eight times as long as wide in the middle; remaining segments fused into a curious, rounded, narrow-necked bulb. Third vein nearly straight; the sinuous apical cross-vein joins third vein a little before the mergence in costa; fifth vein runs to the wing margin. Subgenotype—*Cerioides bulbosa* de Meijere.

Distribution: oriental (Java) 1.

#### MONOCEROMYIA Shannon.

*Monoceromyia* Shannon, *Bull. Brooklyn Ent. Soc.* **17**, 41 (1922).

Cheeks and occiput bulging below. Face straight until it retreats above epistoma. Antennifer long and slender, nearly as long as the antennae. Humeri pilose; scutellum very short; metanotum strongly developed; metasternum pilose. Abdomen much constricted basally, often very slender and usually pointed posteriorly. Hind femora only slightly thickened, with spines posteriorly on lower surface. Anterior wing margin dark, or wing altogether cyaneous; posterior margin somewhat chitimized. Third longitudinal vein looped, but without appendix; apical cross-vein joins third vein at the apex. Genotype—*Cerioides tricolor* Loew.

Distribution: palaearctic 3; nearctic 1; neotropical 5; Ethiopian 13; oriental 20; Australian 6; Oceania 1.

#### THE SUBFAMILY ERISTALINAE.

The Eristalinae constitutes one of the largest groups of the family, containing nearly eight hundred species. They are compact flies with short, convex, rapidly tapering abdomen and large squamae. They are at once distinguished by the looped third vein, in which the kink is usually deep, and the fact that at the base of each femur, especially the hind ones, there is a patch of dense, short, sharp setulae. These setae are also found to some extent in some Xylotinae, Cheilosinae and some Microdontinae. The wing venation of the Eristalinae is suggestive of *Volucella* in the fact that usually the third vein, together with the apical cross-vein, end with the costa a considerable distance above the apex of the wing and, furthermore, like *Volucella* in the inflated abdomen and large squamae, and the frequently closed marginal cell. Different from the *Volucella* is the fact that the sixth vein is strongly bent downward and outward, whereas it is characteristically concave in the Volucellinae, and moreover the plumose arista of *Volucella* is scarcely duplicated even in *Eristalis*. The beginning of the subfamily must go back some distance. Two fossil species of *Helophilus* have been described from the Oligocene; two of *Eristalis*, less well known.

Two fairly well-marked tribes may be recognized. The more generalized of these is the Helophilini with its open submarginal cell, and the Eristalini with its



closed marginal cell which is usually petiolate and the apex often bulbous. The author suspects that the use of this character may sometimes bring together unnatural assemblages in a few instances. For instance, the relationship of *Thalamopales* with its produced front, retreating face and elongate form seems to belong more naturally with *Quichuana* than with *Eristalis*. There is some room to believe that this entire group containing *Quichuana*, *Habromyia*, *Meromacrus*, *Myiatropa* is a plastic group of comparatively recent origin, with *Myiatropa* as the oldest. It may be argued in support of the use of this character of the closed marginal cell that by its use practically all of those genera with dichoptic males are thrown into the Helophilini, and the majority of those with holoptic males go into the Eristalini. Finally it may be pointed out that many of the categories created in the subfamily are based upon minor structural characters and are certainly of only subgeneric value. The group appears to be rather homogeneous on the whole. For the Eristalini the trend might be said to be towards: eyes patterned, front overgrown and callose; scutellum acquiring rim and groove, face gaining tubercle, body changing pile for microsetae, or sometimes tomentum. By tomentum, the author refers to coarse, lustreless, opaque pile. For the Helophilini the trend might be: great size, with long pile, hind femora and tibiae and to a lesser extent the anterior ones, incised, or spurred, toothed, tuberculate, etc.; apical cross-vein recurrent, thorax vittate.

The flies of this subfamily are distributed into one or two phylogeront genera, two tribogenera, twenty-five genera, thirty-three subgenera and two groups (*Priomerus*, *Pleskeola*) which have not been seen by the author.

*A key to the groups of the subfamily Eristalinae.*

- |   |    |                                  |
|---|----|----------------------------------|
| 1. Marginal cell always open.....   | 2  |                                  |
| Marginal cell always closed .....   | 32 |                                  |
| 2. Sixth vein straight and not concave on its anterior face; eyes of male widely dichoptic; face tuberculate; abdomen slenderly oval; loop of third vein moderate only .....  |    | <i>Chasmomma</i> Bezzi.          |
| Sixth vein bowed or curved, concave anteriorly .....  | 3  |                                  |
| 3. Subapical cross-vein strongly recurrent, the kink in the third vein exceptionally deep. Hind femora much thickened. Usually with a definite preapical plate bearing a tooth; usually shaggy, long pilose flies ..... | 4  |                                  |
| Subapical cross-vein never recurrent; hind femora slender or thick, without a plate bearing a tooth .....   | 5  |                                  |
| 4. Male and female arista both simple. The hind femora apically bears a large lateral plate which may have one or more teeth.....   |    | <i>Merodon</i> Meigen.           |
| Male arista distally lamellate; female arista slightly so .....   |    | <i>Platymochaetus</i> Wiedemann. |
| 5. Stigmal cross-vein absent .....  | 6  |                                  |
| Stigmal cross-vein present or in the last stages of development ....  | 10 |                                  |
| 6. Base of hind tibiae rounded and simple; scutellar margin greatly thinned and deeply emarginate .....   |    | <i>Orthoprosopa</i> Macquart.    |
| Base of hind tibiae pinched into a rather sharp, knife-like ventral edge (adjacent to the femur) .....  | 7  |                                  |
| 7. Front remarkably swollen below; claspers especially long .....   |    | <i>Dolichogyna</i> Macquart.     |
| Front not swollen; claspers short .....   | 8  |                                  |
| 8. Face produced diagonally forward as a cone .....   |    | <i>Eurhimyia</i> Bigot.          |
| Face not conically produced forward .....   | 9  | [Curran and Fluke                |
| 9. Base of hind femora with a tooth like spur.....  |    | <i>Prohelophilus</i>             |

- Hind femora without such spur ..... *Helophilus* Meigen.
10. Hind basitarsi with a few to many globuliferous hairs below ; males usually holoptic ..... 11  
 Ventral pile of hind basitarsi simple and setate ; males dichoptic.. 14
11. Midfemora attenuated and with a broad basal tooth and apical kink, the area between deeply incised ; hind femora and tibiae simple. *Eumerosyrphus* Bigot.  
 Midfemora and tibiae simple ..... 12
12. Anterior tibiae greatly enlarged, these tibiae and their femora with great matted tufts of hair ..... *Tityusia* Hull.  
 Anterior tibiae and femora simple ..... 13
13. Hind femora with a small apical plate ; hind tibiae twice excavated. *Prionotomyia* Bigot.  
 Hind femora without an apical plate ; hind tibiae not twice excavated. *Mesembrius* Rondani.
14. The face is usually deeply produced below, the fronto-antennal region never prominent and produced. Rather large, woolly, long pilose flies as a rule (*Mallota* and its subgenera) ..... 15  
 Face not produced below ; fronto-antennal region sometimes prominent. Rather short pilose flies ..... 23
15. Eyes of male strongly dichoptic ..... 16  
 Eyes of male nearly approximated or strongly holoptic. Hind femora strongly thickened and often arcuate ; face not strongly projecting downward ..... 18
16. Hind femora straight and not greatly thickened ; hind tibiae without long, sharp apical spur ; face strongly projecting downward and concave beneath the antennae ..... 17  
 Hind femora thick and arcuate, their tibiae with a very long, sharp, apical spur. Abdomen short pilose ..... *Polydontomyia* Williston.
17. Thorax striped ; abdomen short pilose ; face below conical and attenuate ..... *Arctosyrphus* Frey.  
 Thorax unicolorous ; abdomen densely pilose ; face not attenuated and conical ..... *Mallota* Meigen.
18. Eyes at least in female pilose ; in males touching or barely approximated. Hind femora very thick. Small cross-vein over the middle of the discal cell ..... 19  
 Eyes in both sexes bare ..... 21
19. Hind femora in both sexes equally thick and bent ..... *Paramallota* Shiraki.  
 Hind femora of male extraordinarily thick and bent ..... 20
20. Eyes in both sexes pilose ..... *Imatisma* Macquart.  
 Eyes only pilose in female, in male barely touching ..... *Pseudomallota* Shiraki.
21. Eyes of male clearly holoptic. Hind femora moderately thick ... 22  
 Eyes of male hardly touching. Hind femora of both sexes strongly thickened. Small cross-vein at middle of discal cell. Abdomen long pilose ..... *Pseudomerodon* Shiraki.
22. Small cross-vein at apical third of discal cell ; abdomen short pilose. *Pseudozetterstedtia* Shiraki.  
 Small cross-vein at middle of discal cell ; pile everywhere very short appressed and setaceous ; hind tibiae thick and flattened, arcuate and ending transversely ; tubercle of face prominent ..... *Edwardsiella* Hull.
23. Fronto-antennal region strongly produced forward ; subconical.... 24  
 Fronto-antennal region not so produced ..... 26
24. Abdomen slender and elongate, the first two segments sometimes expanded ..... 25  
 Abdomen of the usual type, rather wide, the slightly narrowed apex usually with a large hypopygium ..... *Criorithrix*, gen. n.



25. Eyes pilose ..... *Quichuana* Knab.  
 Eyes bare ; loop of third vein sometimes with an appendix ..... *Habromyia* Williston.
26. Ocelli wide apart and remote, the ocellar triangle quite large ..... *Asemosyrphus* Bigot.  
 Ocellar triangle small ..... 27
27. Scutellum tuberculate at each side apically ..... *Pilinasica* Malloch.  
 Scutellum non-tuberculate ..... 28
28. Eyes thickly pilose ; males holoptic ; hind femora slender ; face tuberculate ; hind tibiae with median ridge ..... *Myiatropa* Rondani.  
 Eyes bare ..... 29
29. Hind femora massive, arcuate, deeply incised at base ; their tibiae with basal knife-edge, attenuate apically and spurred ; hypopygium large and elongate ; males holoptic ; face tuberculate .. *Tigridomyia* Bigot.  
 Not such flies and the males dichoptic..... 30 [Fluke.
30. Face tuberculate ; small flies ..... *Lunomyia* Curran and  
 Face not tuberculate ; gently concave above, greatly arched or convex below, or face straight in profile ..... 31
31. Abdomen slender and subcylindrical ; especially in the males ..... *Lejops* Rondani.  
 Abdomen broad and comparatively flat ; usually short oval ..... *Parhelophilus* Girschner.
32. Sixth vein quite straight, hind femora slender ; face tuberculate .. *Digulia* de Meijere.  
 Sixth vein strongly bent backward ; concave anteriorly ..... 33
33. Third vein with very little curve or dip and no loop or kink ; abdomen slender, males widely dichoptic ..... 34  
 Third vein with the usual deep kink ..... 35
34. Thorax and abdomen with peculiar flattened pile ..... *Dissoptera* Edwards.  
 Without unusual pile ; face rectangular below in profile, produced equally below and forward and gently concave above ; face quite narrow ..... *Xenozoon*, gen. n.
35. Face drawn out into a long slender cone or porrect snout ..... *Lycastirrhyncha* Bigot.  
 Face not conical and snout-like..... 36
36. Face straight or concave in profile ..... 37  
 Face tuberculate, or concave only upon the upper portion ..... 38
37. Face concave ; curve of third vein moderate, curve of sixth vein pronounced ; hind femora quite slender ; abdomen broad and short ..... *Keda* Curran.  
 Face nearly straight in profile ; abdomen slender and elongate conical. *Palumbia* Rondani.
38. Loop of third vein oblique and elongate upon the proximal slope ; eyes very large, long holoptic, the upper facets enlarged ; hind femora quite slender. Large flies with oval, convex abdomen . *Axona* Wiedemann.  
 Both slopes of the third vein loop quite equal ..... 39
39. Loop of third vein deep and usually appendiculated, the appendix sometimes reduced to a trace or rarely absent ; scutellum large, unusually wide and emarginate ..... 40  
 Loop of third vein broad and rounded and never with appendix ; scutellum rarely emarginate ..... 45
40. Fronto-antennal region greatly produced ; occiput very tumid ; with rectangular margin above ; abdomen elongate and rather slender ..... *Thalamopales*, gen. n.  
 This region not greatly produced ; almost always short, compact flies. 41
41. Stalk or petiole of the marginal cell very short ; eyes with pale whitish spots ; males holoptic ; male vertical triangle long and narrow ; villosity of wings entire..... 42  
 Marginal cell greatly shorter distally than the subcostal cell and with a long stalk ; no pale spots on eyes ..... 43

42. Face with a lateral bulla or tubercle on each side ..... *Triatylus*, subgen. n.  
 Face with only the median tubercle ..... *Senaspis* Macquart.
43. Males holoptic, the facets larger above; head much swollen, with a wrinkled denudose callus upon the lower front; hind femora rather slender; wings in part bare ..... 44  
 Males widely dichoptic; the upper facets small; no frontal callus; hind femora thick; wings villose apically ..... *Simioides* Loew.
44. Hind femora with a spur or plate distally ..... *Dolichomerus* Macquart.  
 Hind femora simple ..... *Megaspis* Macquart.\*
45. Eyes with vertical stripes or spots or both ..... 46  
 Eyes unicolorous ..... 50\*
46. Pattern of eyes chiefly in vertical stripes with sometimes a few spots. 47  
 Pattern of eye in spots and no stripes ..... 48
47. Eye stripes broken up largely into spots; male eyes narrowly separated, but angularly approximated; end of marginal cell bulbous. Hind femora quite thick ..... *Merodonoides* Curran.  
 Eye stripes with few or no spots; males holoptic; marginal cell apex not conspicuously bulbous or not at all expanded; hind femora slender or a little thickened ..... *Eristalodes* Mik.
48. Face sharply conical, produced below and only a little forward; face rather narrow; front of female and its face equally wide; wings wholly avillose ..... *Helophilina* Becker.  
 Face not sharply conical; face wider than front; wings wholly or in part avillose ..... 49
49. Hypopygium enlarged; end of marginal cell quite bulbous ..... *Velocimyia* Hull.  
 Hypopygium not enlarged; end of marginal cell not enlarged .... *Lathyrrophthalmus* Scopoli.
50. Outer edge of scutellum emarginate and creased ..... 51  
 Outer edge of scutellum rounded and convex ..... 52
51. Scutellum large and three times as wide as long; face deeply concave above and the front rather prominent ..... *Solenaspis* Bigot.  
 Scutellum of normal shape and size; front not prominent ..... *Kertezomyia* Shiraki.
52. Basal part of hind tibiae produced into a knife-edge ..... 53  
 Base of tibiae round and simple ..... *Eristalomysia* Rondani.
53. Eyes of male separated ..... *Eristalinus* Rondani.  
 Eyes of male holoptic ..... 54
54. Arista short plumose ..... *Eristalis* Latreille.  
 Arista pubescent or bare ..... *Pseudoeristalis* Shiraki.

## THE TRIBE HELOPHILINI.

All genera and subgenera with the marginal cell open. Characteristically compact species which are seldom slender. Either short pilose or long pilose and bumblebee-like. Eyes bare except in a few genera, under which it is stated. It is true of both subfamilies that the groups are closely related for the most part, but little differentiated and often based upon few characters; I believe that for many of these a subgeneric evaluation comes nearer to expressing the true relationship of these forms. We should probably regard this subfamily as a dominant and

\* *Meromacrus* will normally key out at couplet 50, being separated from remaining genera by the thick spots or fascia of opaque pale tomentum; one or two species have the loop of the third vein appendiculate and these trace to *Megaspis* Macquart and are separated in the same way. All *Megaspis* species are old world; all *Meromacrus* species are new world. Genus revised by Hull, *Amer. Mus. Novitates*, No. 1200 (1942).



## HELOPHILUS Meigen.

*Helophilus* Meigen, *Syst. Beschreibung*, **3**, 338 (1822).

Face slightly concave on upper half, the lower half of face convex, straight, retreating, or with a small tubercle. Third antennal segment approximately orbicular. Eyes bare, dichoptic in male. Face wholly pollinose with bare medial vitta. Usually bright coloured flies of medium size, sometimes small. Femora comparatively slender. Genotype—*Musca pendula* Linnaeus.

Distribution: palaearctic 19; nearctic 11; neotropical 4 (may belong elsewhere); oriental 15; Australian 8; holarctic 1; fossil species 2.

Recognized subgenera: *Pilinasica* Malloch, *N.Z. I. Inst. Sci. Tech.* **5**, 227 (1922). This is a *Helophilus*-like fly in which the scutellum bears a tubercle at each side, much as in *Mallometasternum*. Genotype—*Syrphus cingulata* Fabricius.

Distribution: Australian (New Zealand) 1.

Not recognized: *Prohelophilus* Curran and Fluke, *Trans. Wis. Acad. Sci.* (A. Let.) **22**, 210 (1926), based only upon an elongate, subbasal spur upon the hind femora of male and female (based upon *Syrphus trilineatus* Fabricius).

Not recognized: *Kirimyia* Bigot, *Ann. Soc. Ent. Fr.* (6), **2**, Bull. p. cxxxvi (1882), for *eristoloides* Bigot. Based only upon the non-vittate thorax.

## ASEMOSYRPHUS Bigot.

*Aemosyrphus* Bigot, *Ann. Soc. Ent. Fr.* (6), **2**, Bull. p. cxxviii (1822).

*Helophilus*-like flies; male eyes widely dichoptic. The principal distinctions lie in the three ocelli, which are quite remotely distant from one another, and the stigma which simulates a cross-vein. Hind femora a little more thickened than in *Helophilus*; the mesonotum less vittate. Subgenotype—*Helophilus mexicanus* Macquart.

Distribution: nearctic 2; neotropical 1.

Recognized subgenus: *Lunomyia* Curran and Fluke, *Tr. Wis. Acad. Sci.* (A. Let.) **22**, 252 (1926). Close to *Aemosyrphus*, differing only in the presence of a minute tubercle upon the face, the non-remote ocelli (ocellar triangle small). Hind femora moderately thickened; the stigma simulates a cross-vein. Subgenotype—*Tropidea cooleyi* Seamans.

Distribution: nearctic 2.

## DOLICHOGYNA Macquart.

*Dolichogyna* Macquart, *Dipt. Exot.* **2**, Pt. 2, 65 (1842).

These are distinctive species, a little longer pilose, the abdomen a little more flattened. Distinguished principally by the greatly inflated front, in which the face somewhat shares. Eyes bare, widely dichoptic. Hind femora not greatly thickened. Thorax usually vittate. Stigma simulating a cross-vein. The genus finds a parallel in *Scaeva* and *Styxia* in the Syrphinae. Genotype—*Helophilus chilensis* Walker.

Distribution: neotropical 4.

successful and evolving group at this time, plastic, and in which the phylogenetic trend is in numerous directions. There is a remarkable persistence of the vittate pollinose thorax through many of the Helophilini.

## PARHELOPHILUS Girschner.

*Parhelophilus* Girschner, *Illustr. Wochenschr.* 2, 604 (1897).

Small, short, oval, pollinose-marked flies. Face barely concave beneath the antennae, slightly convex on the lower half; seldom produced but if so produced downward; face wholly pubescent; males dichoptic. Hind femora moderately thickened, sometimes with a basal spur. Stigma simulating a cross-vein. Genotype—*Syrphus frutetorum* Fabricius.

Distribution: palaearctic 2; nearctic 8.

This genus may be considered to rest upon three characters: (a) the stigma, cross-vein type, shared by several groups; (b) the wholly pubescent face; (c) the hind tibia plane apically. These last two distinctions separately could hardly be regarded of great value. The acute hind tibia occurs rather frequently among the Xylotinae where the author has largely disregarded it. *Parhelophilus* then contains two other minor groups, unrelated to one another. *Lejops* and *Eurhimyia*, each removed from *Parhelophilus* by two distinctions, and each of which would be a progeny of a not now existing type, a short faced, oval abdomen fly with spurred tibiae.

*Lejops* (subgenus), *Dipt. Ital. Prodrôme*, 2, 33 (1857).

A *Parhelophilus* in which the hind tibia ends acutely and the abdominal form has become slender and subcylindrical; males dichoptic. Subgenotype—*Mallota vitata* Meigen.

Distribution: palaearctic 2; nearctic 9; Ethiopian 3.

*Eurhimyia* Bigot (subgenus), *Ann. Soc. Ent. Fr.* (6), 3, 226 (1883).

A *Parhelophilus* in which the body has remained oval, but the face is directed diagonally forward into a long cone quite beyond the end of the antennae; it is of a different type from the cone of *Lycastirrhyncha*. The hind tibiae end in a spur. It is possible to regard *Lejops* as a subdivision of *Eurhimyia* or the reverse. Subgenotype—*Rhingia lineata* Fabricius.

Distribution: palaearctic 2; nearctic 1; Ethiopian 1; oriental 1; holarectic 1.

## MESEMBRIUS Rondani.\*

*Mesembrius* Rondani, *Dipt. Ital. Prodrôme*, 2, 50 (1857).

*Helophilus*-like flies in which the eyes of the male are holoptic and which have a patch of globuliferous hairs upon the base or greater part of the hind basitarsi, the number varying from few to many. The face is concave above. Genotype—*Helophilus peregrina* Loew.

Distribution: palaearctic 3; Ethiopian 22; oriental 6; Australian 1.

*Eumerosyrphus* Bigot (subgenus), *Ann. Soc. Ent. Fr.* (6), 2, *Bull.* p. cxxviii (1882).

A *Mesembrius* in which the attenuated mid-femora have a broad tooth and an apical, distalward, posterolateral knob, the area of the femora between the two knobs full; also the mid-tibiae are deeply concave, incised near the middle; hind femora and tibiae normal, the former a little thickened, their basitarsi swollen.

\* *Paramesembrius* Shiraki, *Mem. Fac. Sci. Agric. Taihoku*, 1, p. 176 (1930). This is a subgenus of *Mesembrius* with holoptic eyes. It will run to couplet 22, and is separable by the globuliferous hairs of the hind basitarsi. Subgenotype—*Tubifera abdominolis* Sack.



Face with merest possible tubercle ; the eyes touch for six to eight facets ; stigma simulates a cross-vein. Front completely, densely silver pubescent. Subgenotype—*indianus* Bigot.

Distribution : oriental (Southern Asia) 1.

*Tityusia* Hull (subgenus), *Psyche*, **44**, 118 (1937).

Large, *Mesembrius*-like ; dark coloured. Hind femora but little thickened, their basitarsi with a large thick tuft of hair ; enlarged and thickened anterior femora and very much enlarged anterior tibiae with great long tufts of hair, which are somewhat matted at the apex, much as a wet brush ; second to fourth fore-tarsal segments widened and greatly produced as a slender curved lobe. Face with minute tubercle ; front produced ; second antennal segment a little elongate. Subgenotype—*regulus* Hull.

Distribution : Ethiopian 1.

*Prionotomyia* Bigot (subgenus), *Ann. Soc. Ent. Fr.* (6), **2**, Bull. p. cxxi (1882).

A *Mesembrius*-like fly based solely upon the twice excavated hind tibiae and the slight apical plate of the hind femora. *Prionotomyia* rests then upon very slender grounds. Based on *tarsata* Bigot (Ethiopian ; 3 species).

*Tigridemyia* Bigot (subgenus), *Ann. Soc. Ent. Fr.* (6), **2**, Bull. p. cxxi (1882).

*Teuchomerus* Sack, *Arch. Naturgesch.* **88** A, No. 11, 8 (1922).

A species in which there is a deep, rounded excision from basal fourth to middle of hind femora, the basal side of which is formed by a large, long, sharp but rounded spur ; femora rather thickened ; base of their tibiae knife-like, serrate and excised. Occiput spiculate ; antennae pitted, face with slight tubercle ; no fringe upon scutellum ; loop of third vein not deep ; stigma simulates a cross-vein. Subgenotype—*pictipes* Bigot. No basitarsal globulous hairs.

Distribution : oriental 1.

#### KLOSSIA Curran.

*Klossia* Curran, *J. F.M.S. Mus.* **16**, 370 (1931).

Face with a prominent tubercle upon the lower half, concave above. The tubercle reaches as far as the fronto-antennal prominence ; the epistoma extends no farther than the length of the face at its concavity. Eyes bare. Antennae short ; third segment more or less oval, but with the ventral margin approximately plane. Arista bare. Vittae of thorax weak. Abdomen short oval. Hind femora a little thickened. Loop of third vein not deep ; marginal cell open. Genotype—*Eristalis singularis* Walker (*K. dimidiata* Curran).

Distribution : Malayan 1.

#### LYCOPALE Hull.

*Lycopale* Hull, *J. Wash. Acad. Sci.* **34**, 129 (1944).

*Helophilus*-like flies in which the pile has been replaced by opaque tomentum as in *Meromacrus*. Mesonotum vittate. The abdomen differs from *Helophilus* in being quite convex and subcylindrical ; the base is broad and tapers posteriorly. Hind femora a little thickened. Margin of wings brown ; third vein with strong loop ; marginal cell open. Genotype—*Meromacrus vittata* Hull.

Distribution : neotropical 1.

## CATACORES Hull.

*Catacores* Hull, *Ent. News*, **55**, 205 (1944).

Face tuberculate and concave above; front a little protuberant; epistoma not greatly produced. Antennae short; third segment oval. Eyes large, bare, holoptic. Scutellum with a well-marked marginal crease. Abdomen broad and short. Legs simple; hind femora a little thickened. Third vein with a deep kink; marginal cell widely open; anterior cross-vein at middle of discal cell. Genotype—*Axona cyanea* Brunetti.

Distribution: Indian 1.

## POLYDONTOMYIA Williston.

*Polydonta* Macquart, *Dipt. Exot. Suppl.* **4**, 144 (1850).

*Triodonta* Williston, *Bull. Brooklyn Ent. Soc.* **7**, 136 (1885).

*Polydontomyia* Williston, *Manual N. American Diptera*, 89 (1896).

Face tuberculate, produced deep below, concave above the tubercle, with bare medial stripe. Antennae short, third segment shorter than deep; arista thick. Eyes bare, widely dichoptic but angulated. Scutellar fringe absent. Mesonotum unstriped. Abdomen wide and tapering; hypopygium large. Hind femora greatly thickened and arcuate with large, blunt, apical, setiferous protuberance; tibiae flattened, enlarged, arcuate, knife-like, semi-setate at base, spur very long. Loop of third vein medium deep; stigma simulates a cross-vein. Sexes dimorphic for colour, femora and tibial spurs. Genotype—*Merodon curvipes* Wiedemann.

Distribution: nearctic 1.

## ORTHOPROSOPA Macquart.

*Orthoprosopa* Macquart, *Dipt. Exot. Suppl.* **4**, 143 (1849).

Face long vertically though only moderately produced downward and virtually none forward; face barely concave with a trace of a tubercular convexity in the middle; antennae set high. Face and front pubescent throughout, both with sparse pile. Antennae short, third segment shorter than deep, subtruncate. Eyes bare, holoptic. Thorax without vittae; scutellum with fringe, with thin, creased rim; metasternum pilose. Abdomen elongate oval, short setate with their white bloom. Hind femora moderately thickened but not arcuate; tibiae thickened, arcuate, with rounded base. Loop of third vein rather shallow; stigma elongate. Genotype—*nigra* Macquart.

Distribution: Australian 1.

## EDWARDSIETTA Hull.

*Edwardsiella* Hull, *J. Wash. Acad. Sci.* **31**, 437 (1941).

Face deeply concave above with well-developed tubercle; considerably produced below the tubercle. Head wide, short; front long and quite short; eyes bare (male unknown). Antennae short; third segment longer than wide, obtusely pointed. Abdomen broad, wider than thorax; tapering. Hind femora greatly thickened, slightly concave on basal two-thirds; ventrolateral margin apically



Fig. 24.



setiferous ; tibiae very wide and flattened, arcuate, nearly as long as femora. Loop of third vein quite deep ; sixth vein strongly arched posteriorly ; third vein ends well above wing apex. Genotype—*ochracea* Hull.

Distribution : neotropical (Panama) 1.

#### MYIATROPA Rondani.

*Myiatropa* Rondani, *Nuov. Ann. Sci. Nat. Bologna* (2), 2, 453 (1844).

Face produced somewhat downward, none forward ; face with medial bare stripe and abundant pile. Face with a moderate tubercle in the middle ; barely concave above it ; straight below it. Antennae short, third segment slightly longer than wide. Eyes thick pilose ; holoptic. Scutellar rim convex, without fringe ; metasternum pilose. Abdomen short, wider than thorax, tapering. Hind femora and tibiae slender, latter not knife-edged. Loop of third vein deep ; stigma twice as long as wide. Rather long pilose flies. Genotype—*Musca florea* Linnaeus.

Distribution : palaearctic 5 ; Australian 1.

#### QUICHUANA Knab.

*Quichuana* Knab, *Insec. Inscit. Menstr.* 1, 13 (1913).

Front somewhat produced ; face usually retreating, with a weak tubercle near the middle and bare medial vitta. Antennae elongate upon the third segment, sometimes on all three. Eyes thick, with flattened, shining pile ; holoptic. Thorax thick, opaque, tomentose ; metasternum pilose ; scutellum convex, without fringe. Abdomen usually slender and tapering, sometimes short and oval and convex. Hind femora from little to much thickened, their arcuate, flattened tibiae with knife-edge base. Wings with brown margin, the loop deep, the stigma rather like a cross-vein. Genotype—*sylvicola* Knab.

Distribution : neotropical 21.

#### CRIORTRIX, gen. n.

Face with tubercle, weak or strong, and concave above, deep or shallow ; face below tubercle either subrectangular, or a little produced down ; a medial stripe bare. Eyes bare and holoptic. Fronto-antennal region produced, much or little. Antennae quite often large, third segment may be shorter than deep ; arista thick. Thorax with or without tomentum. Scutellum convex, without fringe ; metasternum pilose. Abdomen wide, subrectangular in females, rather flattened ;

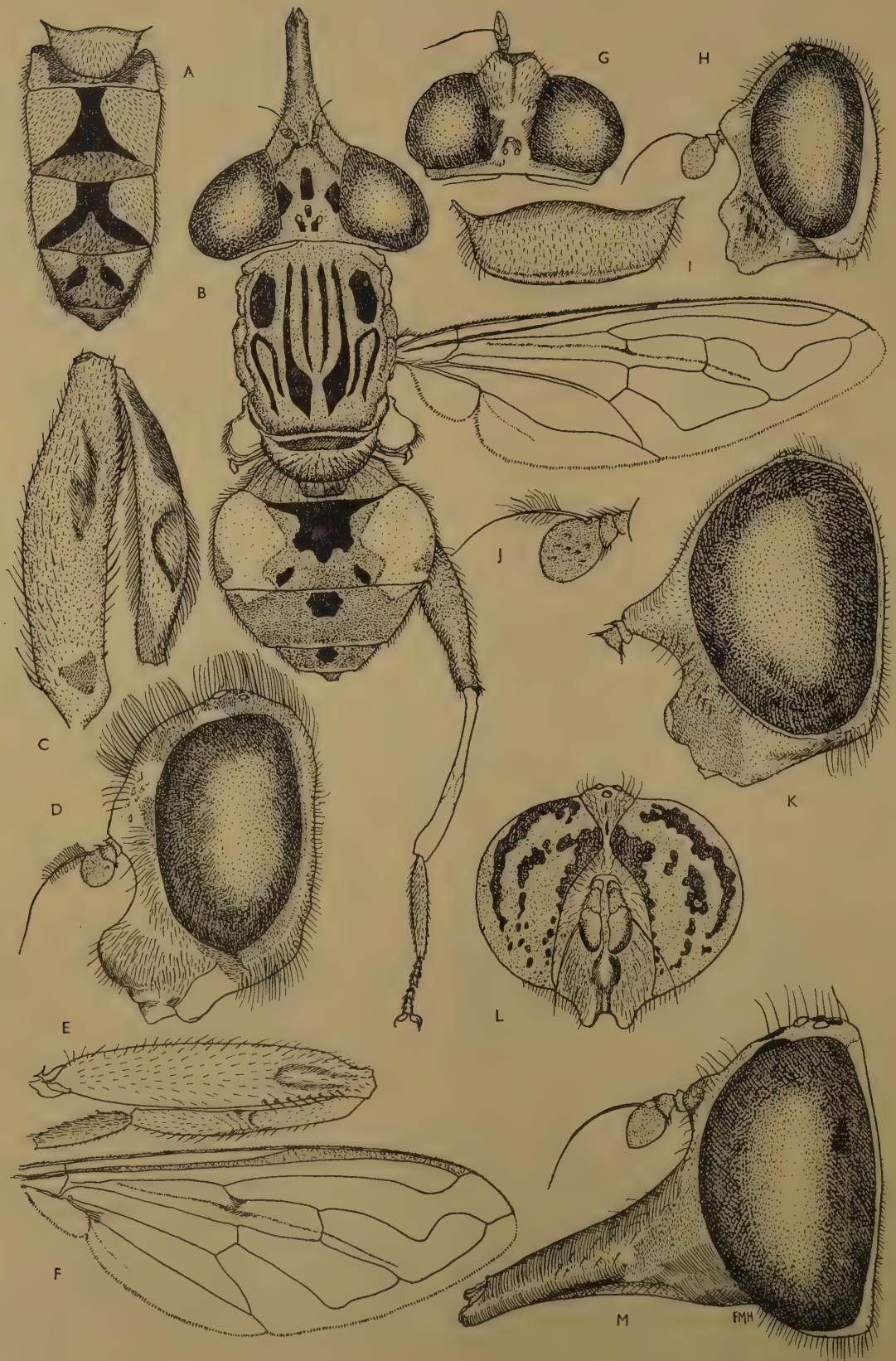
---

#### The Subfamily Eristalinae.

- A. *Habromyia coeruleithorax* Williston, wing ; B. *Velocimyia velox* Hull, wing (type) ; C. *Bomboscelosis coreana* Enderlein, wing (type) ; D. *Pilinasica cingulata* Fabricius, scutellum, lateral view ; E. *Klossia singularis* Walker, profile of head ; F. *Edwardsiella ochracea* Hull, profile of head (holotype) ; G. *Protylocera dibaphus* Walker, profile of head ; H. *Criorthrix magnifica* Bigot, profile of head (type) ; I. *Mesembrius* sp., hind tibia, basitarsus ; J. *Habromyia coeruleithorax* Williston, profile of head ; K. *Helophilina taeniaceps* Becker, profile of head (type series) ; L. *Thalamopales scitus* Walker, profile of head (type) ; M. *Tigridemyia pictipes* Bigot, hind femur ; N. *Arctosyrphus nitidulus* Frey, profile of head.



Fig. 25.



hypopygium large, wide. Femora moderately to much thickened, not arcuate; tibiae flattened, arcuate, serrate knife-edged. Wings with brown margin; stigma cross-vein-like; third vein loop deep. Genotype—*Habromyia rectilinea* Hull.

Distribution: neotropical 3.

#### HABROMYIA Williston.

*Habromyia* Williston, *Trans. Amer. Ent. Soc.* **15**, 284 (1888).

*Meromacrus*-like flies in which the abdomen is quite elongate and subcylindrical especially in the male; it is elongate, somewhat flattened, slightly narrowed in the middle in the female; male eyes narrowly dichoptic. Loop of third vein deep, angulate, regularly with a spur in the female (in genotype). Genotype—*coeruleithorax* Williston.

Distribution: neotropical 5.

#### CHASMOMMA Bezzi.

*Chasmomma* Bezzi, *Syrph. Ethiopian Region*, 102 (1915).

Face long, straight, with a prominent tubercle in both male and female. Antennae short; third segment elongate, about one and a half times longer than wide. Eyes bare; widely dichoptic in males. Scutellum with margin. Abdomen elongate-oval, rather narrow. Hind femora considerably thickened with spinose setae below; hind tibiae arched and much shorter than femora. Loop of third vein only moderate or even shallow; first posterior cell petiolate; sixth vein quite straight. They are short pilose, rather bare, dark flies. Genotype—*femoratum* Bezzi. The author examined the type series at the British Museum; the patches of setae at the base of each femur throw this species into the Eristalinae and not the Xylotinae where Bezzi placed it.

Distribution: Ethiopian 2.

#### MALLOTA Meigen.

*Mallota* Meigen, *Syst. Beschreibung*, **3**, 377 (1822).

Face quite deeply produced, the deep cheeks sloping into the cylindrical, obtuse cone of the lower part of face; upper face concave, below with a long, low convexity, front produced. Antennae short; the third segment much shorter than wide; Occiput very thick and tumid. Eyes long, densely pilose; widely dichoptic. Abdomen stout, short oval. Hind femora rather slender and only little thickened; their tibiae flattened and somewhat arcuate. Loop of third vein deep; in all forms the stigma simulates a cross-vein. These are large, thick, long pilose, woolly, bumblebee-like flies. Genotype—*Syrphus fuciformis* Fabricius.

---

#### The Subfamily Eristalinae.

- A. *Digulia kochi* de Meijere, abdomen (type); B. *Lycastirrhyncha nitens* Bigot, dorsal view; C. *Solenaspis nitens* Bigot, hind femur and tibia (type); D. *Simioides crassipes* Loew, profile of head; E. *Digulia kochi* de Meijere, hind femur and tibia (type); F. *Digulia kochi* de Meijere, wing (type); G. *Digulia kochi* de Meijere, head from above (type); H. *Digulia kochi* de Meijere, profile of head (type); I. *Solenaspis nitens* Bigot, scutellum (type); J. *Eristalomys tenax* Linnaeus, antenna; K. *Solenaspis nitens* Bigot, profile of head (type); L. *Merodonoides czernyi* Hull, front of head (type); M. *Lycastirrhyncha nitens* Bigot, profile of head.



Distribution: palaearctic 12; nearctic 10; neotropical 13; Ethiopian 6; oriental 8; holarctic 1.

The species of this large genus vary considerably in the shape of the face, antennae, femora, and the length and extent of pile. Female femora less developed. Eyes in some tending towards and reaching holopticism; there are several subgenera and related genera.

*Imatisma* Macquart (subgenus), *Dipt. Exot.* II, 2, 67 (1842).

*Mallota*-like flies in which the hind femora are extraordinarily bent and thickened and the eyes touch narrowly or for a short distance. Eyes sparsely pilose in both sexes. Face a little produced diagonally forward but more below; deeply concave above; tubercle large. Third antennal segment suborbicular, anterior cross-vein over the middle of the discal cell. Subgenotype—*orientalis* Macquart.

Distribution: palaearctic 1; nearctic 1; oriental 1.

*Pseudomallota* Shiraki (subgenus), *Mem. Fac. Sci. Agric. Taihoku*, 1, 187 (1930).

*Mallota*-like flies in which the female eye only is pilose, the male eye holoptic. Subgenotype—*Mallota tricolor* Loew.

Distribution: palaearctic 1.

*Paramallota* Shiraki (subgenus), *Mem. Fac. Sci. Agric. Taihoku*, 1, 191 (1930).

Similar to *Mallota*. Hind femora equally thick and bent in both sexes. Eyes pilose. Anterior cross-vein over the middle of the discal cell. Subgenotype—*Mallota haemorrhoidalis* Sack.

Distribution: oriental 3.

*Bombozelosis* Enderlein, *S.B. Ges. naturf. Fr. Berl.* 136 (1934).

Very near if not identical with *Paramallota* Shiraki. I have carefully studied and drawn the type in the Berlin Museum and I find very few differences. Erected by Enderlein for *coreana* Enderlein.

*Pseudozetterstedtia* Shiraki (subgenus), *Mem. Fac. Sci. Agric. Taihoku*, 1, 199 (1930).

Eyes of male clearly holoptic; eyes bare. Femora moderately thick; anterior cross-vein at apical third of discal cell. Abdomen short pilose. Subgenotype—*unicolor* Shiraki.

Distribution: palaearctic 1.

*Pseudomerodon* Shiraki (subgenus), *Mem. Fac. Sci. Agric. Taihoku*, 1, 189 (1930).

Eyes of male barely touching; eyes bare. Hind femora of both sexes strongly thickened; anterior cross-vein at middle of discal cell; long pilose flies. Subgenotype—*Mallota takasagoensis* Matsumura.

Distribution: palaearctic 1.

#### ARCTOSYRPHUS Frey.

*Arctosyrphus* Frey, *Acta Soc. Fauna Flora Fenn.* 46, 15 (1919).

Face concave above, but very deeply produced below into a narrow pointed cone. Third antennal segment subquadrate. Eyes bare, widely dichoptic. Abdomen

elongate-oval. Hind femora a little thickened through the middle; tibiae not noticeably flattened, about five-sixths length of femur. Anterior cross-vein just beyond middle of discal cell; sixth vein strongly bent backward. Quite short pilose, obscurely vittate flies. Genotype—*nitidulus* Frey.

Distribution: palaearctic (Yakutzs) 1.

#### MERODON Meigen.

*Merodon* Meigen, *Illiger Mag. f. Insektenkunde*, 2, 274–77 (1803).

Face concave with projecting epistoma; long pilose, with bare medial stripe. Epistomal production often slight, hence face markedly retreating. Antennae short, the third segment sometimes a little elongated. Eyes pilose; holoptic. Scutellum with prominent creased rim and ventral fringe; metasternum pilose. Abdomen stout, wide and short oval; usually convex. A few species are more slender and taper markedly. Hind femora greatly thickened, often arcuate, with very prominent lateral, apical ventral plate; tibiae thick, heavy, short and very frequently excised in one or more places, or with thorny spurs or protuberance. Wings characteristic; loop of third vein large and deep; third vein ending well above wing apex; apical cross-vein strongly recurrent; first posterior cell long petiolate; anterior cross-vein at middle of discal cell; stigma simulates a cross-vein. These flies range from long, thick, woolly, pilose species to short, nearly bare, pollinose, fasciate flies; large to small in size. Genotype—*Syrphus clavipes* Fabricius.

Distribution: palaearctic 104; neotropical 1 (probably belongs elsewhere); Ethiopian 10; oriental 4; Australian 1; fossil species 1.

*Platynochaetus* Wiedemann (subgenus), *Zweifl. Insekt.* 2, 147 (1830).

*Merodon*-like flies in which the arista of the male is expanded and flattened distally. Subgenotype—*Syrphus setosus* Fabricius.

Distribution: palaearctic 5.

*Exmerodon* Becker (subgenus), *Annu. Mus. Zool. Acad. St. Péterb.* 17, 606 (1912).

A *Merodon* based upon a number of minor differences in the shape of the antennal segment and the degree of dichopticism. The third vein was said to be but little bent, the straight hind femora little thickened with hardly any projecting enlargement. Subgenotype—*fulcratus* Becker.

Distribution: palaearctic 1.

#### THE TRIBE ERISTALINI.

Marginal cell closed; almost always short pilose flies.

#### ERISTALIS Latreille.

*Eristalis* Latreille, *Hist. Nat. Crust. Insect.* 14, 363 (1804).

Face tuberculate, concave upon the upper half to a varying extent and a little produced downward and diagonally forward, the amount also varying. The antennae are short; the third segment usually a little longer than wide. Typically the third segment is apt to be longest ventrally and there plane, while, dorsoapically,



it is shorter and rounded ; arista long and short plumose basally in *Eristalis* s. str., bare or microscopically pubescent basally in different subgenera. The eyes range from bare to pilose (s. str.), with or without bare bands, from unicolorous (s. str.) to dark vertical bands or numerous spots upon a lighter ground colour. The eyes are holoptic (s. str. and others), or narrowly separated on one subgenus. Mesonotum short ; scutellum convex, without rim, with ventral fringe. Squamae large. Abdomen short and compact and rather convex. Hind femora slender to moderately thickened and without spurs or spines or teeth ; apically the ventral margin is often setiferous ; tibiae nearly straight or moderately arcuate. Marginal cell of wing closed ; loop of third vein deep ; sixth vein strongly bent backwards ; anterior cross-vein at or near middle of discal cell ; third vein ends well above the apex of the wing. Genotype—*Musca arbustorum* Linnaeus.

Distribution : palaearctic 32 ; nearctic 49 ; neotropical 123 ; Ethiopian 20 ; oriental 103 ; Australian 14 ; oceania 2 ; holarctic 5 ; fossil species 3.

The species of this large and yet rather homogeneous assemblage vary in numerous minor respects. Some of these deserve minor group values. The flies are short pilose for the most part. Generally short pilose flies, although there are groups of long woolly species ; colours dull or bright. Size medium, occasionally large and rarely small.

Recognized subgroups :

*Eristalinus* Rondani (subgenus), *Nuov. Ann. Sci. Nat. Bologna* (2), **2**, 453 (1844).

Eyes of male distinctly separated. Small species with slender femora. Subgenotype—*Musca sepulchralis* Linnaeus.

Distribution : palaearctic 1 ; nearctic 2.

*Eristalomyia* Rondani (subgenus), *Dipt. Ital. Prodrôme*, **2**, 38 (1857).

Arista bare or microscopically pubescent, eyes pilose with one or more bare stripes. Medium-sized species, otherwise *Eristalis*-like. Subgenotype—*Musca tenax* Linnaeus.

Distribution : palaearctic 4 ; the subgenotype cosmopolitan.

*Pseudoeristalis* Shiraki (subgenus), *Mem. Fac. Sci. Agric. Taihoku*, **1**, 147 (1930).

*Eristalis* species with eyes bare and bare or micropubescent arista. Subgenotype—*bicolor* Shiraki.

Distribution : palaearctic.

*Lathyrophthalmus* Scopoli (subgenus), *Wien Ent. Ztg.* **14**, 114 (1894).

Eyes with numerous, small, dark spots, usually without pile. Hind femora slender to moderately thickened. Medium-sized species, many of which are metallic. Subgenotype—*conops aenea* Scopoli.

Distribution : palaearctic 1 ; a few others perhaps in southern Europe ; Ethiopian 20 ; oriental 10 ; Australian several ; oceania 1 ; holarctic 1 ; the subgenotype is holarctic.

*Helophilina* Becker (subgenus), *Denkschr. Akad. Wiss. Wien* **198**, 68 (1923).

*Sarnia* Curran, *Bull. Amer. Mus. Nat. Hist.* **57**, 73 (1927).

Eyes with small spots ; bare. Small flies with narrow face and front which are about the same width (in female) ; lower face rather sharply conical ; femora

simple. Subgenotype—*taeniaticeps* Becker (*Sarnia* Curran for *Eristalis smaragdinus* Macq.)

Distribution : Ethiopian 2.

*Eristalodes* Mik (subgenus), *Wien Ent. Ztg.* **16**, 114 (1897).

Eyes with four or five vertical, irregular stripes, bare or pilose. Hind femora slender or moderately thickened. Subgenotype—*Eristalis taeniops* Wiedemann.

Distribution : palaearctic, perhaps one or two species ; Ethiopian 9 ; oriental 2.

*Velocimyia* Hull (subgenus), *Psyche*, **44**, 13 (1937).

Eyes spotted ; bare. Abdomen broad basally, tapering to the very large hypopygium. Hind femora greatly swollen, arcuate, with ventral, lateral, apical, setiferous plate ; tibiae flattened, apically dentate, as long as the femora, basally serriform knife-edged, distal to which is an excision. Apex of marginal cell bulbous. Subgenotype—*velox* Hull.

Distribution : Ethiopian 2.

*Kertezomyia* Shiraki (subgenus), *Mem. Fac. Sci. Agric. Taihoku*, **1**, 151 (1930).

*Eristalis*-like flies in which the scutellum is margined. Femora rather slender. Face tuberculate ; arista pubescent ; femora rather slender. Metallic species. Subgenotype—*Eristalis violascens* Kertesz.

Distribution : palaearctic (Japan, Formosa) 1.

*Merodonoides* Curran (subgenus), *J. F.M.S. Mus.* **16**, 333 (1930).

Eyes bare, with irregular stripes, more or less broken into spots. Eyes in male barely touching. Abdomen wide, tapering to the large hypopygium. Hind femora greatly thickened. Genotype—*Helophilus singularis* Walker (*M. circularis* Curran).

Distribution : oriental 3.

#### DIGULIA de Meijere.

*Digulia* de Meijere, *Nova Guinea*, **9**, 357 (1913).

A remote genus. Eyes bare, unicolorous (male unknown). Face tuberculate, concave above, lower face developed forward slightly but none downward, the epistoma as far forward as the tubercle ; third antennal segment oval and rounded ; occiput prominent and rectangularly tumid throughout abdomen elongate-oval. Hind femora simple and only slightly thickened throughout ; apically with a row of small spines below ; tibiae slender, a little more than two-thirds as long as femur, their apex plane. Loop of third vein not as deep as in *Eristalis* and tending towards the type found in *Korinchia*. Sixth vein quite straight. End of marginal cell slightly expanded. Anterior cross-vein at middle of discal cell ; third vein ending shortly above wing apex ; first posterior cell rather long petiolate. Genotype—*Kochi* de Meijere.

Distribution : oriental 1.

The most important characteristic in this fly is the quite straight sixth vein : it is possible that it should be regarded as a subgenus of *Korinchia*, and that it does not belong to the *Eristalinae*.



## MEROMACRUS Rondani.

*Meromacrus* Rondani, *Truqui Studi Entomol.* 1, 70, p. iii, f. 305 (1848).

Face concave above, without tubercle, but convex and prominent below; not produced downward. Fronto-antennal region protuberant or at least prominent. Third antennal segment usually elongate-oval; arista long, bare. Eyes bare, holoptic. Abdomen broad and compact, tapering to the large hypopygium. Femora from slender to much thickened, tibiae flattened, arcuate, shorter than femora, with basal knife-edge. Third vein with deep loop; sixth vein very strongly bent backward; apex of anal cell attenuate. Anterior cross-vein transverse, and somewhat beyond middle of discal cell; wings usually with a brown anterior border. Large shining flies with bright spots or fascia of opaque tomentum. Genotype—*ghiliani* Rondani.

Distribution: nearctic 2; neotropical 33.

## SENASPIS Macquart.

*Senaspis* Macquart, *Dipt. Exot. Suppl.* 4, 437 (1851).

*Protylocera* Bezzi, *Ann. Mus. Civ. Genoa*, 5, 415 (1912).

Face strongly tuberculate, deeply concave above. Antennae short, third segment elongate oval or oblique oval dorsally; arista bare. Eyes bare, holoptic, with pale spots, vertical triangle of male long and narrow. Fronto-antennal region quite prominent. Squamae quite large. Abdomen broad and rather flattened, except apically in the males. Hind femora considerably thickened with a short, low, apical, lateral, ventral, setiferous plate; their tibiae much flattened, shorter than femora, ending plane and with basal knife-edge. Loop of third vein sloping; it tends to be angular below and often with short appendix. Marginal cell tends to be narrowly closed, the petiole of first posterior cell usually short, the vein ending shortly above wing apex; anterior cross-vein beyond middle of discal cell to as far as discal third; sixth vein strongly bent backward. These are larger, quite bare, thick microsetate flies of characteristic appearance. Wings usually brown or banded. Genotype—*flaviceps* Macquart.

Distribution: Ethiopian 13.

*Triatylus*, new subgenus.

Those species with a large rounded tubercle on either side of the face besides the medial one. Subgenotype—*Xylota dibaphus* Walker.

Distribution: Ethiopian 1.

## MEGASPIS Macquart.

*Megaspis* Macquart, *Dipt. Exot.* 2, 2, 27, (1842).

*Phytomia* Guérin, *Bélangier Voyage Indes Orient* (7), 509 (1834), pr. Halliday.

*Pachycephalus* Weidemann, *Aussereurop. Zweifl. Ins.* 2, 152 (1830). No type designation.

Face shallowly concave, with low, long tubercle. Head much swollen. Front never produced, quite long and circular in profile, the antennae placed low upon the head, and with a large, bare, rugose spot over antennae. Eyes large and bare; holoptic, often with dark horizontal bands; facets larger above in the male.

Antennae short; third segment elongate oval, rounded dorsally; arista bare. Squamae large. Abdomen short and compact and convex; usually with bullae, weak or strong, upon terminal segments. Hind femora slender with sometimes an apical lateral plate. Wings entirely or almost without pubescence; sixth vein strongly bent; petiole of marginal and first posterior cells long; third vein ending above apex of wing. The genotype differs in the minor respect of the presence of an oblique ridge which ventrally margins the facial concavity. Genotype—*Eristalis chrysopygus* Wiedemann.

Distribution: Ethiopian 21; oriental 8.

*Dolichomerus* Macquart (subgenus), *Dipt. Exot. Suppl.* 4, 131 (1849).

A *Megaspis* in which the hind femora bear a strong subapical tooth. Subgenotype—*Syrphus crassus* Fabricius. Approached by *M. neavei* Bezzi.

Distribution: Ethiopian 2; oriental 1.

#### SIMIOIDES Loew.

*Simioides* Loew, *Ofvers. Kgl. Vet. Akad. Forh.* 14 (1857).

Face deeply concave and strongly, convexly protuberant on lower half into which the tubercle may be called merged. Antennae short; arista plumose basally. Eyes bare, angulated and dichoptic in male. Hind femora more strongly thickened than in *Megaspis*; apex of wing with pubescence in the middle. Related to *Megaspis*. Bezzi states that the eyes have two faint, dark, sinuous stripes; they seem wanting in my specimens. Some of the African species of *Mallota* are closely related. Genotype—*crassipes* Loew.

Distribution: palaearctic 1; Ethiopian 2.

#### SOLENASPIS Osten-Sacken.

*Solenaspis* Osten-Sacken, *Ann. Mus. Civ. Genoa*, 16, 442 (1881).

Face deeply concave, the fronto-antennal region much produced and the tubercle below quite prominent. Head subglobular. Eyes large, bare. Scutellum extremely broad, three or more times as wide as long, subrectangular and with a deep rim; without ventral fringe. Abdomen very broad, widest basally, pointed or tapering apically, rather convex, but the lateral margins flattened. Hind femora moderately thickened, with a ventral lateral row of seta-like bristles but no plate. Hind tibiae considerably enlarged and flattened especially in the middle; apex plane. Venation as in *Eristalis*. Inter-related with *Kertezomyia* or perhaps with the *Senaspis* stem. Genotype—*Plagiocera nitens* Bigot.

Distribution: oriental 1.

#### MEROMACROIDES Curran.

*Meromacroides* Curran, *Bull. Amer. Mus. Nat. Hist.* 57, 69 (1927).

Face deeply concave above, with a prominent tubercle united with the epistoma. Fronto-antennal region prominent. Antennae short; third segment elongate oval. Eyes pilose; angular and dichoptic in the male. Abdomen elongate and nearly cylindrical and tapering posteriorly. Hind femora greatly thickened, setiferous below; their tibiae arcuate. Loop of third vein deep, narrow, angular below, the



basal branch straighter and more vertical than the distal branch. Anterior cross-vein a little beyond middle of discal cell ; sixth vein strongly bent. Genotype—*Eristalis meromacriiformis* Bezzi.

Distribution : Ethiopian 1.

#### AXONA Wiedemann.

*Axona* Wiedemann, *Proc. Linn. Soc. Lond.* **12**, 211 (1864).

A phylogeront. Head large. Eyes bare and exceedingly extensive, occupying most of head, and holoptic for a long distance ; upper facets enlarged ; no eye spots ; front small. Face concave above, tuberculate below. Antennae short ; third segment rounded apically and deeper than long ; arista bare. Scutellum a little thinned apically but without rim ; without fringe. Abdomen large, wide, elongate, oval, shallowly convex, and short setate ; lateral margins rather flattened as in *Senaspis*. Hind femora quite slender upon the apical half, and slightly thickened basally ; their tibiae quite slender, rounded basally. Venation rather like *Eristalis* ; petiole of marginal and first posterior cell long ; third vein ending well above wing apex ; sixth vein much bent, anal cell attenuate ; loop of third vein moderate, the fore branch oblique from the beginning of the cell, the distal branch more vertical. *Axona* appears to be related to *Senaspis*. Genotype—*Eristalis chalcopyga* Wiedemann.

Distribution : oriental 1.

#### KEDA Curran.

*Keda* Curran *J. F.M.S. Mus.* **16**, 331 (1930).

Face evenly concave between the antennae and the slightly produced epistoma ; no tubercle. Eyes large, bare, holoptic. Antennae short. Third segment elongate oval ; arista bare. Abdomen short, oval, compact. Hind femora and tibiae quite slender. Loop of third vein very shallow ; sixth vein strongly bent ; marginal cell narrowly closed ; petiole of first posterior cell long ; its vein ending well above apex of wing ; anterior cross-vein at middle of discal cell. Genotype—*simpliciceps* Curran.

Distribution : oriental 1.

#### PALUMBIA Rondani.

*Palumbia* Rondani, *Atti Soc. Ital. Sci. Nat. Milano*, **8**, 129 (1865).

Face concave between antennae and epistoma, the latter produced a little forward ; no tubercle. Eyes bare, holoptic. Occiput well developed, with a subrectangular margin. Calli of thorax and thorax opposite wing with many long, stiff bristles. Scutellum with fringe. Abdomen rather slender, wider at base, tapering to the large hypopygium. Hind femora only a little thickened, with short, thick, stubby bristles on each side apically ; hind tibiae a little curved, the apex plane. Loop of third vein characteristic ; the basal branch is long with gradual descent, beginning near base of cell (as in *Axona*), the discal branch with abrupt rise and slightly recurrent ; bottom rounded, without appendix ; end of third vein far above wing apex. Genotype—*Sphyxea bellieri* Bigot.

Distribution : palaearctic (S. Europe) 1.

## DISSOPTERA Edwards.

*Dissoptera* Edwards, *Trans. Zool. Soc. Lond.* 20, 410 (1915).

Face concave between antennae and epistoma, the latter produced twice as far from the eyes as the front; no tubercle. Antennae large and short; third segment a little longer than wide, flattened above, arista bare. Eyes bare, or short pilose; widely dichoptic in males. Occiput strongly thickened behind ocelli; narrow laterally. Thorax densely golden scalose, giving it a very beautiful appearance. Humeri and pleura tomentose; scutellum long pilose and scalose. Abdomen broad at the base, quite thick and inflated on some species, with large yellow spots and scalose pile; in others slender and subcylindrical and non-scalose. Loop of third vein shallow; third vein ends practically at wing tip. Genotype—*pollinosa* Edwards.

Distribution: oriental 2; Australian 1.

## THALAMOPALES, new genus.

Fronto-antennal region greatly produced. Face retreating, without tubercle, the epistoma not produced. Head short but wider than the thorax. Eyes bare (male unknown). Occiput thick, with rectangular edge. Second and third antennal segments somewhat elongated. Abdomen as wide basally as thorax but quite elongate. Hind femora moderately thickened, the ventral apex with stiff setae; tibiae slender, arcuate, knife-edged at base. Marginal cell of wing closed and petiolate; loop of third vein moderately deep and rounded, V-shaped. Mesonotum with yellow tomentose pattern. This form is perhaps nearest *Meromacrus*, with elongate abdomen and produced front. Genotype—*Helophilus scitus* Walker.

Distribution: neotropical (Amazon) 1.

## LYCASTRIRRHYNCHA Bigot.

*Lycastriirrhyncha* Bigot, *Rev. Mag. Zool.* (2), 11, 307 (1859).

A phylogeront. Face about the epistoma drawn out into a long, slender, porrect cone, as long as in *Rhingia*. Antennae short; third segment about as long as wide, a little pointed. Eyes bare; widely dichoptic. Abdomen short; compact; short oval. Hind femora a little thickened; hind tibiae slender, slightly arcuate and rounded basally, nearly as long as femur. Marginal cell closed and petiolate; first posterior cell long petiolate, its vein ending above wing apex; sixth vein bent backward a little; anterior cross-vein at middle of discal cell; loop of third vein deep. Genotype—*Rhingia nigra* Macquart.

Distribution: neotropical 5.

## XENOZON, new genus.

Face quite narrow, concave above, dropping straight down to the rectangular epistoma. Antennae short, third segment a little shorter than wide. Eyes bare, widely dichoptic. Head wider than thorax. Metasternum pilose. Abdomen slender, narrow, tapering and subcylindrical apically. Hind femora and tibiae quite slender, the former with basal setae. Marginal cell of wing closed and short petiolate; third vein almost without curve, the dip or loop quite shallow, the vein



ending at apex of wing ; first posterior cell with a fairly long stalk ; the apical cross-vein joins third vein at an acute angle, the perfectly transverse anterior cross-vein joins fourth vein at basal fourth of discal cell. Sixth vein bent backwards somewhat ; anal cell attenuate ; no stigmal cross-vein. Pile of fly of medium length and erect. Related to *Dissoptera* Edwards it differs in the shape of the face and the fact that its pile is in no way peculiar. Genotype—*Dissoptera maritima* Hull. Distribution : Oceania 1.

#### PRIOMERUS Macquart.

*Priomerus* Macquart, *Hist. Nat. Ins. Dipt.* 1, 511 (1834).

“ Face prominent, a little concave beneath antennae ; epistoma thick, descending some distance below eyes in profile. Eyes holoptic in male. Antennae on a frontal projection ; third segment oval ; arista bare, dorsal. Abdomen depressed. Hind femora denticulate. Marginal cell closed.” Genotype—*fasciatus* Macquart. Distribution : “ India ”.

Unknown to the author, and also to Brunetti, the author of the ‘ Fauna of British India ’. By some, it has been placed in *Eristalis*, but apparently without actual study. Macquart placed it close to *Helophilus*. Another species was placed here from the neotropical region and one from the palaearctic region, but the relationships and value of the genus is not understood.

#### PLESKEOLA Stackelberg.

*Pleskeola* Stackelberg, *Wien Ent. Ztg.* 41, 25 (1924).

Face tuberculate ; eyes of male dichoptic ; third vein with a shallow bend. The author has not seen the species upon which the genus was founded ; not illustrated by Stackelberg. Genotype—*sibirica* (from Siberia).

#### PROMILESIA Arribalzaga.

*Promilesia* Arribalzaga, *Ann. Soc. Cient. Argent.* 33, 241 (1892).

A medium-sized fly with bare eyes and elongate antennae. The head is quite high, that is, it is long vertically, but quite short anteroposteriorly. The face is somewhat produced downward and has a rather abrupt, decided concavity just above its middle and below the antennae. The face is without tubercle although the lower half is rounded in profile. The first segment of the antenna is short, the second a little longer, the third nearly twice as long as the first two segments and with dorsal arista. Sides of the face with pubescence. Abdomen oval or subconically ovate. Hind femora thickened or incrassate. Wings hyaline, briefly fuscous along the margin.

Upon the wings the submarginal cell has the posterior angle briefly appendaged. This fly has not been re-studied since its original description, nor has the author seen it. The above is a brief translation of the description. Genotype—*nectarinoides* Arribalzaga.

Distribution : neotropical (Argentina) 1.

*Palaeoeristalis* Hull (fossil genus). Characterized by: being *Eristalis*-like flies with short robust abdomen. Venation like *Eristalis* except the third vein has only a gentle curve. Hind femora very much thickened and setate. Genotype—*tessellatus* Hull.

Not recognized: *Streblia* Enderlein (based on *Megaspis natalensis* Macq.); *S.B. Ges. naturf. Fr. Berl.* 237 (1937).

This was based entirely upon the enlarged upper male ommatidia, which are separated from the lower one by a line of demarcation.

Not recognized: *Metalloeristalis* Kanervo, *Ann. Univ. Turkuensis* (Ser. A.) 6, 13 (1938).

The author rejects this name, based as it was upon genitalia with styles of a certain shape. Either way it is considered, it appears unfortunate to destroy older classification to erect a new one, or to resort to a system which must necessarily result in a multiplicity of minor categories. In 1925 the author studied the genitalia of *Eristalis* at some length, concluding at that time that these structures furnished useful supporting characters where specific characters are vague. *Metalloeristalis* was based upon *aenea* Scopoli, which is already the type of *Lathyrrophthalmus*.

Not recognized: *Eoseristalis* Kanervo, *Ann. Univ. Turkenensis* (Ser. A.) 6, 12 (1938).

I do not recognize this name (based upon *Eristalis cerealis* Fabr.) for the reasons given above; it seems to the author that the numerous configurations of the genitalia lend confusion to the general problem of generic classification, because of the complicated shape and form of these structures.

While it is possible to pick out striking types, as is at once evident from the studies of Metcalf (1921), one may raise the question as to whether a classification based upon these shapes will be any more stable and satisfactory than one based upon external evidence.

#### GENERA INCERTIS SEDAE.

##### GALLICERA Portevin.

*Gallicera* Portevin, *Ency. Ent.* (Ser. 3) 2, *Dipt.* 4, Paris, p. 15 (1927).

The author has not seen the description of this fly.

#### BIBLIOGRAPHY.

- BEZZI, MARIO (1915). The Syrphidae of the Ethiopian Region, pp. 1-146. British Museum (Nat. Hist.).
- BRUES, C. T. (1929). Present Trends in Systematic Entomology. *Psyche*, 36, 13-20.
- BRUES, C. T. (1933). Progressive Change in the Insect Populations of Forests Since the Early Tertiary. *Amer. Nat.* 67, 385-406.
- BRUNETTI, E. (1923). *The Fauna of British India*.—Diptera, 3.
- CHAMBERLAIN, J. C. (1924). The Hollow Curve of Distribution. *Amer. Nat.* 58, 350-374.
- COCKERELL, T. D. A. and LEVEQUE (1932). The Antiquity of Insect Structures. *Amer. Nat.* 65, 351-359.
- COQUILLET, D. W. (1910). The Type Species of North American Genera of Diptera. *Proc. U.S. Nat. Mus.* 37, 499-622.



- CURRAN, C. H. (1923). Relation of the Biological and Taxonomic Characters in Syrphidae. *Rept. Ent. Soc. Ontario*, p. 30.
- CURRAN, C. H. (1924). Concerning the Availability of Taxonomic Characters. *Psyche*, **31**, pp. 167-169.
- CURRAN, C. H. (1924). Contribution to a Monograph of the Syrphidae (Diptera) from North of Mexico. *Kans. Univ. Sci. Bull.* **15**, 1-216.
- CURRAN, C. H. (1928). The Syrphidae of the Malay Peninsula. *J. F.M.S. Mus.* **14**, 141-324.
- CURRAN, C. H. (1934). *The Families and Genera of North American Diptera*. Ballou Press, pp. 1-512.
- CURRAN, C. H. (1938-1939). Records and Descriptions of African Syrphidae, Parts I to IV. *Amer. Mus. Nov.* **1009**, **1010**, **1025**, **1026**.
- CURRAN, C. H. and FLUKE, C. L. (1926). Revision of the Nearctic Species of *Helophilus* and Allied Genera. *Trans. Wis. Acad. Sci. Arts Lett.* **22**, 207-281.
- DIXEY, F. A. (1908). On Müllerian Mimicry and Diaposematism. *Trans. Ent. Soc. Lond.* **1908**, 559-583.
- EFFLATOUN, H. C. (1922). A Monograph of Egyptian Diptera.—Part I. Fam. Syrphidae. *Mem. Soc. Ent. Egypte*, **2**, 1-123.
- EPLING, CARL (1939). An Approach to Classification. *Sci. Monthly*, **1939**, October, 350-367.
- FERGUSON, E. W. (1926). Revision of Australian Syrphidae.—Parts I & II. *Proc. Linn. Soc. N.S.W.* **51**, 137-163 ; 517-544.
- FERRIS, G. F. (1928). *The Principles of Systematic Entomology*. Stanford Univ. Press.
- FISHER, R. A.; WILLIAMS, C. B. and CORBET, A. S. (1943). Forecasting the Number of Lice on the Lousy. *Monthly Sci. News*, **29**, 3-4.
- FLUKE, C. L. (1933). Revision of the Syrphus Flies of America North of Mexico.—Part I. *Trans. Wis. Acad. Sci. Arts Lett.* **28**, 63-127.
- FLUKE, C. L. (1935). Revision of the Epistrophe Flies of America North of Mexico. *Ent. Amer.* **15**, 1-57.
- FLUKE, C. L. (1942). Revision of the Neotropical Syrphini. *Amer. Mus. Nov.* **1201**, 1-24.
- FLUKE, C. L. (1945). The Melanostomini of the Neotropical Region. *Amer. Mus. Nov.* **1272**, 1-29.
- GIRSCHNER, E. (1897). Über die Postalar-Membrane (Schüppchen, Squamulae) der Dipteren. *Ill. Wschr. Ent.* **2**, 534.
- HULL, F. M. (1925). A Review of the Genus *Eristalis*.—Parts I & II. *Ohio J. Sci.* **11-43** ; 285-310.
- HULL, F. M. (1929). The Syrphidae of the Samoan Islands. *Insecta Samoanensis*. (Survey of London School of Tropical Medicine), pp. 191-198. British Museum (Nat. Hist.).
- HULL, F. M. (1935). Description of new species of the Genus *Sphegina* with a Key to those known from North America. *Trans. Amer. Ent. Soc.* **61**, 373-382.
- HULL, F. M. (1936). A Check List of the Described Syrphidae from Australia and the Regional Islands. *J. F.M.S. Mus.* **18**, 190-212.
- HULL, F. M. (1937). A Check List of the Syrphidae of Oceania. *Occ. Pap. Bishop Mus. Honolulu*, **13**. (*Pacific Ent. Surv. Publ.* **10**.)
- HULL, F. M. (1943). The Genus *Mesogramma* ; The New World Species of the Genus *Baccha*. *Ent. Amer.* **23**, 1-99.
- HULL, F. M. (1945). A Study of the Fossil Flies of the Family Syrphidae. *Bull. Mus. Comp. Zool. Harv.* **95**, 253-355.
- HULL, F. M. (1948). The Genus *Baccha* from the New World. *Ent. Amer.* **27**, 89-291.
- HUXLEY, J. S. (1932). *Problems of Relative Growth*. Dial Press, N.Y.C.
- HUXLEY, J. S. (1942). *Evolution, the Modern Synthesis*. Harper & Brothers.
- KANERVO, ERKKI (1938). Zur Systematik and Phylogenie der West-Palaearktischen *Eristalis*-Arten (Dipt. Syrphidae) mit einer Revision derjenigen Finnlands. *Ann. Univ. Turkuensis (Series A)*, **61**, No. 4, 1-54.
- KERTESZ, C. (1910). *Catalogues Dipteorum Hucusque Discriptorum*, **7**. *Syrphidae, Dorylaidae, Phoridae, Clythiidae*. Museum Nationale Hungaricum. Budapestini.
- LUNDBECK, WM. (1916). *Diptera Danica*, **5**. Copenhagen.
- MAYR, ERNST (1942). *Systematics and the Origin of Species*. Columbia University Press.
- MCATEE, W. L. (1926). Insect Taxonomy : Preserving a Sense of Proportion. *Proc. Ent. Soc. Wash.* **28**, 68-70.
- MELANDER, A. L. and BRUES, C. T. (1932). Classification of Insects. *Bull. Mus. Comp. Zool. Harv.* **73**, 1-669.

- METCALF, C. L. (1921). The Genitalia of Male Syrphidae. *Ann. Ent. Soc. Amer.* **14**, 169-228.
- METCALF, Z. P. (1937). How the Taxonomist Names the Animals. *Sci. Monthly*, **1937**, 515-523.
- OSBORN, H. F. (1931). New Conceptions of Species and Genera and of Classification, Discovered in the Evolution of the Titanotheres. *J. Mammal.* **12**, 1-12.
- OSBORN, H. F. (1934). The Dual Principles of Evolution. *Science*, **80**, 601, 605.
- OSBORN, H. F. (1934). Aristogenesis, the Creative Principle in the Origin of Species. *Amer. Nat.* **68**, 193-235.
- OSTEN-SACKEN, C. R. (1894). On the Atavic Index Characters. *Berl. Ent. Z.* **39**, 69-76.
- PEARSE, A. S. (1939). *Animal Ecology*. McGraw Hill.
- SACK, PIUS (1928-1932). *Lindner: Die Fliegen der Palaearktischen Region*, **31**, 1-451.
- SACK, PIUS (1930). *Die Tierwelt Deutschlands und der angrenzenden Meeresteile*, Teil **20**, IX. Syrphidae-Conopidae, 1-142.
- SHANNON, R. C. (1921-22). A Re-classification of the Subfamilies and Genera of North American Syrphidae. *Bull. Brooklyn Ent. Soc.* **16**, 65-72, 120-128; **17**, 30-42.
- SHANNON, R. C. and AUBERTIN, D. (1933). *Diptera of Patagonia and South Chile*.—Part 6, Fasc. 3, 120-175. British Museum (Nat. Hist.).
- SHIRAKI, T. (1930). Die Syrphiden des Japanischen Kaiserreichs mit Berücksichtigung benachbarter Gebiete. *Mem. Fac. Sci. Agric. Taihoku*, **1**, 1-446.
- TELFORD, H. S. (1939). The Syrphidae of Minnesota. *Tech. Bull. Univ. Minn. Agric. Exper. Sta.* **140**, 1-76.
- VERRALL, G. H. (1901). *British Flies*, **8**. Platypezidae, Pipunculidae and Syrphidae of Great Britain. London.
- WHEELER, W. M. (1928). *The Foibles of Insects and Men*. New York.
- WILLISTON, S. W. (1886). Synopsis of the North American Syrphidae. *Bull. U.S. Mus.* **31**, 1-335.
- WILLISTON, S. W. (1908). *North American Diptera*. 3rd Ed., New Haven.

## INDEX.

*The Recognized Groups of Syrphidae together with recent Synonymy.*

	Page		Page
<i>Achaonius</i> Munro .....	292	<i>Bombozelosis</i> Enderlein .....	394
<i>Afrosyrphus</i> Curran .....	302	<i>Brachyopa</i> Meigen .....	329
<i>Alipumilio</i> Shannon .....	333	<i>Brachypalpus</i> Macquart .....	362
<i>Allobaccha</i> Curran .....	296	<i>Bulboscrobia</i> Gaunitz .....	353
<i>Allograpta</i> Osten-Sacken .....	293	<i>Cacoceria</i> Hull .....	371
<i>Allograptina</i> Enderlein .....	293	<i>Cacogaster</i> Hull .....	341
<i>Amphoterus</i> Bezzi .....	321	<i>Cacomylia</i> Hull .....	371
<i>Antlops</i> Enderlein .....	290	<i>Callicera</i> Panzer .....	341
<i>Apophysophora</i> Williston .....	348	<i>Calliprobola</i> Rondani .....	368
<i>Archalia</i> Hull .....	341	<i>Calostigma</i> Shannon .....	295
<i>Archimierodon</i> Hull .....	312	<i>Carposcalis</i> Enderlein .....	300
<i>Arctolepta</i> Hull .....	340	<i>Cartosyrphus</i> Shannon .....	327
<i>Arctophila</i> Schiner .....	353	<i>Catacores</i> Hull .....	389
<i>Arctosyrphus</i> Frey .....	394	<i>Ceratophya</i> Wiedemann .....	314
<i>Argentinomyia</i> Arribáizaga .....	302	<i>Ceriatatrix</i> , subgen. n. ....	381
<i>Aristosyrphus</i> Curran .....	316	<i>Ceriogaster</i> Williston .....	367
<i>Asarcina</i> Macquart .....	292	<i>Ceriodes</i> Rondani .....	380
<i>Asemosyrphus</i> Bigot .....	386	<i>Ceriomicrodon</i> Hull .....	314
<i>Asiodidea</i> Stackelberg .....	291	<i>Cervicorniphora</i> Hull .....	317
<i>Atrichosticha</i> Enderlein .....	296	<i>Chaetochelosis</i> Enderlein .....	328
<i>Axona</i> Wiedemann .....	400	<i>Chalcomylia</i> Williston .....	340
<i>Azpeytia</i> Walker .....	321	<i>Chalcosyrphus</i> Curran .....	340
<i>Baccha</i> Fabricius .....	294	<i>Chamaesphegina</i> Shannon .....	339
<i>Bardistophus</i> Mann .....	309	<i>Chamaesyrphus</i> Mik .....	343
<i>Betasyrphus</i> Matsumura .....	286	<i>Chasmia</i> Enderlien .....	293



	Page		Page
<i>Chasmodon</i> Bezzi.....	393	<i>Eristalis</i> Latreille .....	395
<i>Cheilosia</i> Meigen .....	326	<i>Eristalodes</i> Mik .....	397
<i>Cheilosialepta</i> Hull .....	340	<i>Eristalomyia</i> Rondani.....	396
<b>Cheiroxylota</b> , subgen. n. ....	361	<i>Eristalosyrphus</i> Matsumura .....	285
<i>Chilomyia</i> Shannon .....	327	<i>Eumerosyrphus</i> Bigot .....	387
<i>Chrysidimya</i> Hull.....	309	<i>Eumerus</i> Meigen .....	319
<i>Chrysogaster</i> Meigen .....	331	<i>Eumicrodon</i> Curran .....	308
<i>Chrysosomidia</i> Curran.....	368	<i>Eumyiolepta</i> Shannon .....	340
<i>Chrysotoxum</i> Meigen .....	304	<i>Eupeodes</i> Osten-Sacken .....	285
<i>Citibaena</i> Walker.....	319	<i>Eurhimya</i> Bigot .....	387
<i>Clavaplumula</i> Shannon .....	293	<i>Euryepistrophe</i> Szilady .....	294
<i>Cnemodon</i> Egger .....	331	<i>Eusyrphus</i> Matsumura .....	284
<i>Coeloprosope</i> Macquart.....	334	<i>Exmerodon</i> Becker .....	395
<i>Condidea</i> Coquillett.....	352	<i>Fazia</i> Shannon .....	293
<i>Conosyrphus</i> Frey .....	285	<i>Ferdinandea</i> Rondani .....	328
<i>Conosyrphus</i> Matsumura .....	285	<i>Gallicera</i> Portevin .....	403
<i>Copestylus</i> Macquart .....	347	<i>Graptomyza</i> Wiedemann.....	350
<i>Crepidomyia</i> Shannon.....	368	<i>Habromyia</i> Williston.....	393
<i>Crioprora</i> Osten-Sacken .....	374	<i>Hadromyia</i> Williston .....	374
<i>Criorrhina</i> Meigen.....	372	<i>Halictomyia</i> Shannon .....	330
<b>Criorthrix</b> , gen. n. ....	391	<i>Hammerschmidtia</i> Schummel.....	329
<i>Cynorhina</i> Williston .....	369	<i>Hardimyia</i> Ferguson.....	375
<i>Cynorhinella</i> Curran .....	329	<i>Helophilus</i> Meigen .....	361
<i>Cyphipelta</i> Bigot .....	303	<i>Helophilina</i> Becker .....	396
<i>Dasycheilosia</i> Enderlein .....	328	<i>Helophilus</i> Meigen .....	386
<i>Dasyepistrophe</i> Szilady .....	286	<i>Hemilampra</i> Macquart .....	322
<i>Dasysyrphus</i> Enderlein.....	285	<i>Hemixylota</i> Shannon and Aubertin .....	375
<i>Deineches</i> Walker .....	373	<i>Heryngia</i> Rondani.....	330
<i>Desmetrum</i> Enderlein .....	335	<i>Heterepistrophe</i> Szilady.....	294
<i>Dexiosyrphus</i> Hull.....	318	<i>Hiatomyia</i> Shannon .....	327
<i>Didea</i> Macquart .....	291	<i>Hiratanu</i> Matsumura .....	300
<i>Dideoides</i> Brunetti .....	291	<i>Hybobathus</i> Enderlein .....	288
<i>Dideoopsis</i> Matsumura .....	292	<i>Hypselosyrphus</i> Hull.....	317
<i>Digulia</i> de Meijere .....	397	<i>Imatisma</i> Macquart .....	394
<b>Dioprosope</b> , subgen. n. ....	296	<i>Ischiodon</i> Sack .....	290
<i>Disoptera</i> Edwards .....	401	<i>Ischyroptera</i> Pokorny .....	345
<i>Dolichognyna</i> Macquart .....	386	<i>Ischyrosyrphus</i> Bigot .....	286
<i>Dolichomerus</i> Macquart .....	399	<i>Karosyrphus</i> Matsumura .....	286
<i>Doliomyia</i> Hull .....	319	<i>Keda</i> Curran .....	400
<i>Doros</i> Meigen .....	291	<i>Kerteziomyia</i> Shiraki.....	397
<i>Edwardsiella</i> Hull .....	389	<i>Kirimya</i> Bigot .....	386
<i>Emmyia</i> Klocker .....	331	<i>Klossia</i> Curran.....	388
<i>Endoiasimyia</i> Bigot .....	327	<i>Korinchia</i> Edwards .....	362
<b>Eocheilosia</b> , subgen. n. ....	327	<i>Kryptopyga</i> Hull .....	310
<b>Eorhingia</b> , subgen. n. ....	341	<i>Lathyrophthalmus</i> Scopoli .....	396
<b>Eosalpingogaster</b> , subgen. n. ....	299	<i>Lejops</i> Rondani .....	387
<i>Eoseristalis</i> Kanervo .....	403	<i>Lepidopsis</i> Curran .....	347
<i>Eoxylota</i> Hull .....	375	<i>Lepidostola</i> Mik .....	333
<i>Epistrophe</i> Walker .....	292	<b>Leucopodella</b> , subgen. n. ....	296
<i>Episyrphus</i> Matsumura .....	294	<i>Leucozona</i> Schiner .....	286
<i>Eriophora</i> Philippi .....	372	<i>Liochrysogaster</i> Stackelberg .....	332
<i>Eriozona</i> Schiner .....	292		
<i>Eristalinus</i> Rondani .....	396		

	Page		Page
<i>Liogaster</i> Rondani .....	332	<i>Oligorhina</i> Hull .....	298
<i>Lunomyia</i> Curran and Fluke .....	386	<i>Omegasyrphus</i> Giglio-Tos .....	309
<i>Lycastirrhyncha</i> Bigot .....	401	<i>Ornidia</i> St. Fargeau and Serville .....	348
<i>Lycastris</i> Walker .....	374	<i>Ortholophus</i> Bigot .....	367
<i>Lycopale</i> Hull .....	388	<i>Orhoneura</i> Macquart .....	332
<i>Macrometopia</i> Philippi .....	373	<i>Orthoprosopa</i> Macquart .....	389
<i>Macrosyrphus</i> Matsumura .....	284	<i>Pachysphyria</i> Enderlein .....	300
<i>Macrozelima</i> Stackelberg .....	361	<i>Palaeoascia</i> Meunier .....	334
<i>Malayomyia</i> Curran .....	292	<i>Palaeoeristalis</i> Hull .....	403
<i>Malometasternum</i> Shannon .....	368	<i>Palaeopipiza</i> Meunier .....	321
<i>Mallota</i> Meigen .....	393	<i>Palaeosphegina</i> Meunier .....	335
<i>Masarygus</i> Brethes .....	316	<i>Palaeoxylota</i> Hull .....	361
<i>Megametopon</i> Giglio-Tos .....	350	<i>Palumbia</i> Rondani .....	400
<i>Megaspis</i> Macquart .....	398	<i>Papiliomyia</i> Hull .....	316
<i>Megatricon</i> Johnson .....	321	<i>Paragus</i> Latreille .....	301
<i>Megaxylota</i> Hull .....	375	<i>Paramallota</i> Shiraki .....	394
<i>Melangyna</i> Verrall .....	300	<i>Paramesembrius</i> Shiraki .....	387
<i>Melanostoma</i> Schiner .....	299	<i>Paramicrodon</i> de Meijere .....	317
<i>Merapioidus</i> Bigot .....	373	<i>Paramixogaster</i> Brunetti .....	311
<i>Merodon</i> Meigen .....	395	<i>Paramixogasteroides</i> Shiraki .....	311
<i>Merodonoides</i> Curran .....	397	<i>Pararctophila</i> Hervé-Bazin .....	353
<i>Meromacroides</i> Curran .....	399	<i>Parasyrphus</i> Matsumura .....	284
<i>Meromacrus</i> Rondani .....	398	<b>Paratropidia</b> , gen. n. ....	363
<i>Mesembrius</i> Rondani .....	387	<i>Parhelophilus</i> Girschner .....	387
<i>Mesogramma</i> Loew .....	286	<i>Parocryptamus</i> Shirkai .....	311
<i>Metalloeristalis</i> Kanervo .....	403	<i>Pelecinobaccha</i> Shannon .....	296
<b>Metallograptia</b> , subgen. n. ....	293	<i>Pelecocera</i> Meigen .....	343
<i>Metasyrphus</i> Matsumura .....	285	<i>Penium</i> Philippi .....	331
<b>Metepistrophe</b> , subgen. n. ....	293	<i>Petersina</i> Enderlein .....	300
<i>Microdon</i> Meigen .....	308	<i>Phalacrodira</i> Enderlein .....	294
<i>Milesia</i> Latreille .....	370	<i>Phalacromyia</i> Rondani .....	348
<i>Mimocalla</i> Hull .....	295	<i>Philippimyia</i> Shannon .....	374
<i>Mitrosphen</i> Enderlein .....	290	<i>Phytomyia</i> Guérin .....	398
<i>Mixogaster</i> Macquart .....	314	<i>Pia</i> Philippi .....	329
<i>Monoceromyia</i> Shannon .....	381	<i>Pilinasica</i> Malloch .....	386
<i>Mutillimyia</i> Hull .....	372	<i>Pipiza</i> Fallen .....	330
<b>Myiacerapis</b> , subgen. n. ....	309	<i>Pipizella</i> Rondani .....	331
<i>Myiolepta</i> Newman .....	339	<i>Pipunculosyrphus</i> Hull .....	295
<i>Myiatropa</i> Rondani .....	391	<i>Planes</i> Rondani .....	361
<i>Myxogasteroides</i> Shiraki .....	317	<i>Platycheirus</i> St. Fargeau and Serville ....	301
<i>Nannomyrmecomomyia</i> Hull .....	318	<i>Platynochaetus</i> Wiedemann .....	395
<i>Nausigaster</i> Williston .....	322	<i>Plesia</i> Macquart .....	332
<i>Neoascia</i> Williston .....	335	<i>Pleskeola</i> Stackelberg .....	402
<i>Nepenthosyrphus</i> de Meijere .....	364	<i>Pocota</i> St. Fargeau and Serville .....	374
<i>Nephomyia</i> Matsumura .....	328	<i>Pogonosyrphus</i> Malloch .....	370
<i>Neples</i> Porter .....	361	<b>Polistoceria</b> , subgen. n. ....	380
<i>Nosodepus</i> Speiser .....	373	<i>Polybiomyia</i> Shannon .....	380
<i>Nothomicrodon</i> Wheeler .....	318	<i>Polydontomyia</i> Williston .....	389
<i>Ocyptamus</i> Macquart .....	294	<i>Portevinia</i> Goffe .....	329
<i>Odyneromyia</i> Shannon and Aubertin ....	335	<i>Posthonia</i> Enderlein .....	300
<i>Olbiosyrphus</i> Mik .....	290	<i>Posthosyrphus</i> Enderlein .....	286
<i>Oligeriops</i> Hull .....	310	<i>Primocerioides</i> Shannon .....	379
		<i>Priomerus</i> Macquart .....	402



	Page		Page
<i>Prionotomyia</i> Macquart .....	388	<i>Spheginoides</i> Szilady .....	334
<i>Prohelophilus</i> Curran and Fluke .....	386	<i>Sphymorphoides</i> Shiraki .....	379
<i>Promilesia</i> Arribalzaga .....	402	<i>Spilomyia</i> Meigen .....	370
<i>Protoceratophya</i> Hull .....	314	<i>Stenochilosia</i> Matsumura .....	327
<i>Protochrysotoxum</i> Hull .....	304	<i>Stenomicrodon</i> Hull .....	311
<b>Protograptomyza</b> , subgen. n. ....	351	<i>Stenopipiza</i> Matsumura .....	331
<b>Protolepidostola</b> , subgen. n. ....	333	<i>Sterphus</i> Philippi .....	369
<i>Protorhingia</i> Hull .....	341	<i>Stilbosoma</i> Philippi .....	369
<i>Protylocera</i> Bezzi .....	398	<i>Stipomorpha</i> Hull .....	311
<i>Psarus</i> Latreille .....	376	<i>Streblia</i> Enderlein .....	403
<i>Pseudoeristalis</i> Shiraki .....	396	<i>Styloceria</i> Enderlein .....	380
<i>Pseudomallota</i> Shiraki .....	394	<i>Styxia</i> Hull .....	296
<i>Pseudomerodon</i> Shiraki .....	394	<i>Syngenicomyia</i> Becker .....	353
<i>Pseudomicrodon</i> Hull .....	311	<i>Syritta</i> St. Fargeau and Serville .....	364
<i>Pseudopipiza</i> Hull .....	330	<i>Syrittosyrphus</i> Hull .....	363
<i>Pseudosphegina</i> Hull .....	334	<i>Syrphidis</i> Goffe .....	285
<i>Pseudovolucella</i> Shiraki .....	353	<i>Syrphinella</i> Hervé-Bazin .....	317
<i>Pseudozetterstedtia</i> Shiraki .....	394	<i>Syrphipogon</i> Hull .....	309
<i>Psilota</i> Meigen .....	333	<i>Syrphus</i> Fabricius .....	284
<i>Pterallastes</i> Loew .....	375	<i>Tachinosyrphus</i> Hull .....	350
<i>Pterygophoromyia</i> Shannon .....	379	<i>Taeniochilosia</i> Oldenberg .....	327
<i>Ptileuria</i> Enderlein .....	296	<i>Takaomyia</i> Hervé-Bazin .....	335
<i>Ptilobactrum</i> Bezzi .....	310	<i>Talahua</i> Fluke .....	301
<i>Ptilocephala</i> Hull .....	351	<b>Tanaopicera</b> , subgen. n. ....	311
<i>Pyritis</i> Hunter .....	355	<i>Tapetomyia</i> Fluke .....	355
<i>Prypohoena</i> Schiner .....	301	<i>Tatuomyia</i> Shannon .....	367
<i>Quichuana</i> Knab .....	391	<i>Temnostoma</i> St. Fargeau and Serville .....	371
<i>Rhingia</i> Scopoli .....	340	<i>Tenthredomyia</i> Shannon .....	379
<i>Rhinobaccha</i> de Meijere .....	299	<i>Teuchocnemis</i> Osten-Sacken .....	362
<i>Rhinoprosopa</i> Hull .....	298	<i>Teuchomerus</i> Sack .....	388
<i>Rhinotropidia</i> Stackelberg .....	363	<b>Thalamopales</b> , gen. n. ....	401
<i>Rhodendorfia</i> Smirnov .....	302	<i>Therantha</i> Hull .....	295
<i>Rhoga</i> Walker .....	316	<i>Tigridomyia</i> Bigot .....	388
<i>Rhopalosyrphus</i> Giglio-Tos .....	312	<i>Tityusia</i> Hull .....	388
<i>Rhysops</i> Williston .....	300	<i>Toxomerus</i> Macquart .....	286
<i>Salpingogaster</i> Schiner .....	299	<b>Triatylosis</b> , subgen. n. ....	398
<i>Sarnia</i> Curran .....	396	<i>Trichopsomyia</i> Williston .....	330
<i>Sarolepta</i> Hull .....	340	<i>Triglyphus</i> Loew .....	331
<i>Scaeva</i> Fabricius .....	285	<i>Tropidia</i> Meigen .....	367
<i>Senaspis</i> Macquart .....	398	<i>Tuberculanostoma</i> Fluke .....	301
<i>Senoceria</i> Hull .....	367	<i>Ubristes</i> Walker .....	311
<i>Senogaster</i> Macquart .....	364	<i>Valdivia</i> Shannon .....	339
<i>Sericolepta</i> Hull .....	340	<i>Velocimyia</i> Hull .....	397
<i>Sericomyia</i> Meigen .....	352	<i>Viereckomyia</i> Curran .....	348
<i>Simioides</i> Loew .....	399	<i>Volosyrpha</i> Shannon .....	348
<i>Simosyrphus</i> Bigot .....	291	<i>Volucella</i> Geoffroy .....	347
<i>Solenaspis</i> Osten-Sacken .....	399	<i>Volucellosia</i> Curran .....	348
<i>Somula</i> Macquart .....	369	<i>Xanthandrus</i> Verrall .....	299
<i>Sonanomyia</i> Shiraki .....	327	<i>Xanthogramma</i> Mik .....	290
<i>Spathiogaster</i> Rondani .....	296	<b>Xenozoon</b> , gen. n. ....	401
<i>Sphaerophoria</i> St. Fargeau and Serville ..	294	<i>Xylota</i> Meigen .....	361
<i>Sphecomyia</i> Latreille .....	371	<i>Xylotomima</i> Shannon .....	361
<i>Sphegina</i> Meigen .....	334	<i>Xylotodes</i> Shannon .....	362
<i>Spheginascia</i> Meunier .....	328	<i>Xylotosyrphus</i> Hull .....	375
<i>Spheginobaccha</i> de Meijere .....	318		

*The Study of a Generalized Marsupial* (*Dasy cercus cristicauda* Krefft). By  
FREDERIC WOOD JONES, D.Sc., F.R.S., F.Z.S., *Royal College of Surgeons,*  
*London.*

(Plates I and II ; with 99 figures in the text.)

[Received May 25th, 1948.]

CONTENTS.	Page
Taxonomy and External Characters .....	409
Habits, Life History and Ecology .....	418
Osteology. Skull. ....	422
Dentition .....	431
Appendicular Skeleton .....	434
Myology .....	440
Apparatus Digestorius .....	465
Apparatus Respiratorius .....	474
Angiology .....	481
Apparatus Urogenitalis .....	486
Reproductive System. Female .....	486
Reproductive System. Male .....	490
Central Nervous System .....	493
Ductless Glands .....	499
Parasites .....	500
Bibliography .....	501

# EXTERNAL CHARACTERS.

## Genus DASYCERCUS Peters, 1875.

1867. *Chaetocercus* Krefft, *Proc. Zool. Soc. Lond.*, 1866, p. 434, 25 April, 1867. Haplotype,  
*C. cristicauda* Krefft. Not *Chaetocercus* G. R. Gray, 'Cat. Gen. Subgen. Birds', 1855, p. 22.  
1875. *Dasy cercus* Peters, *S.B. Gesell. Naturf. Freunde, Berlin*, 1875, p. 73. New name for *Chaeto-*  
*cercus cristicauda* Krefft.  
1919. *Amperta* Cabrera, 'Gen. Mamm.', p. 65. New name for *Chaetocercus* Krefft.

The generic name *Chaetocercus* of Krefft, being preoccupied by an avian genus, stood in need of revision and Oldfield Thomas accordingly ('Catalogue of the Marsupialia and Monotremata in the collection of the British Museum', 1888, p. 276, and *Ann. Mus. Stor. Nat. Genova* (2) 4, p. 509, 1887) placed the animal in the comprehensive genus *Phascogale*, although he thoroughly appreciated the distinctions of its dental and cranial characters. In 1919 Angel Cabrera, being still further impressed by its generic distinctions, created the genus *Amperta* for its reception ('Genera Mammalium', 1919, p. 65, pl. v, fig. 4.). This generic term is taken from the name by which the animal is known to the natives of Charlotte Waters, Central Australia. As a generic name, however, it cannot stand, since it is antedated by *Dasy cercus*, employed by Peters in 1875, which has therefore been restored.



The Crest-tailed, or Krefft's Pouched Mouse, was first described by Gerard Krefft, Curator of the Australian Museum, Sydney. The original description was published in 1866 (*Proc. Zool. Soc. Lond.*, 1866, p. 435, pl. xxxvi) and is repeated in Krefft's 'Mammals of Australia' of 1871. The generic characters are defined as follows :

"*Chaetocercus*, gen. nov. This new genus, which will conclude the small Dasyuridae of Australia, has been founded upon a very singular animal, approaching in its dentition *Dasyurus* proper much more than any other known genus, and may be defined as follows :

Dasyuridae with short, broad, almost triangular head and strongly developed auditory bulla, which equals that of *Phascogale penicillata* in size. Canine teeth in upper jaw strong and elongate, not so broad at the base as in the genus *Phascogale*. Incisors long and narrow as in *Dasyurus*; the first pair directed forwards, and slightly longer than the others. Premolars three in the upper jaw, the middle one largest, the first somewhat smaller and the last very diminutive and tubercular. Molars of the usual triangular form, with rather blunt tubercles, increasing in size from the first to the third, the fourth being narrow and transverse. The lower jaw is short and strong, and the articulating condyle placed still higher comparatively than in any other species of this group. The incisors are three in number, the first pair being the largest. Canines smaller than those of the upper jaw, but sharp and pointed, without the broad base common to the other small Dasyures. Of premolars only two are found in the lower jaw, the second larger than the third. There are four molars, the first and last being the smallest, the two middle ones of about equal size; on the first the anterior tubercle is scarcely indicated, showing with the absent third premolar, a close approach to the genus *Dasyurus*. Tail thick, compressed, with a crest of black hair upon its apical half, similar to the tail of *Choeropus*".

In his 'Mammals of Australia' published in 1871, the description of the generic characters is amended. Of the premolars of the lower jaw it is said, "the first larger than the second", instead of "the second larger than the third", which must have been included in the original description in error.

The original specimen upon which Krefft founded his species was forwarded to the Australian Museum, Sydney, by F. G. Waterhouse of the (then) Institute Museum of Adelaide. It was said to have been taken in "South Australia, probably the neighbourhood of Lake Alexandrina". This provenance of the specimen is extremely doubtful, since *Dasyurus* is typically an inhabitant of the arid and semi-arid Centre and has since been obtained only from such an environment, no specimens having been subsequently recorded from localities within 200 miles of the Coorong Lakes.

The original specimen was, as Krefft acknowledged, "not in very good condition". It was mounted in the Australian Museum, but, as Spencer records ('Report on the work of the Horn Scientific Expedition to Central Australia', 1896, Part 2, p. 20), "the taxidermist of that time (as Mr. Etheridge is also of opinion) evidently endeavoured to make amends for the lack of fur by inserting patches borrowed from some other beast of as nearly as possible the same colour and texture, but the result is not a success". This seems to be a mild method of

describing a specimen of which "one hind foot measures 18 and the other 24 mm.". It can only be said of Krefft's original figure (pl. 36, *Proc. Zool. Soc. Lond.*, 1866, here reproduced as Pl. II, fig. 1) that it depicts an animal so unlike *Dasyercus cristicauda* that Spencer was justified in describing it as a figure "which could not in certain respects (as to the tail and the coloration) have fairly represented the animal".

When Oldfield Thomas issued his British Museum Catalogue in 1888, he was forced to give, in a condensed form, the original description of Krefft, for in the interval no further specimens had been obtained and the type remained unique. In condensing Krefft's account of the dental characters, Thomas failed somewhat to convey the original author's description of the canines, for Krefft noted that the upper canines were strong and elongate and that those of the lower jaw were somewhat smaller, while Thomas dismisses all the canines as being slender.

It was only in 1896 that additional specimens were described by Baldwin Spencer. These specimens were received from Mr. Byrne of Charlotte Waters and were described in the publication of the Horn Expedition. Spencer gives the measurements of 16 adult specimens of both sexes and the material at his disposal was therefore ample for guaranteeing his amended description of the species (Vol. 2, p. 19) and his figure of the animal (pl. I, fig. 1, here reproduced as Pl. II, fig. 2). Spencer's description of the animal is as follows:

"Size large. Form strong. Fur close and soft, mainly composed of underfur. The general body colour is mouse-grey, tinged with rufous on the back. The under surface is white or cream-coloured, and so are the inner and anterior faces of the limbs and the upper surfaces of the hands and feet. The underfur on the back is slate-grey at the base and rufous terminally; on the ventral surface it is cream-white terminally. The tail is thickly covered in its proximal half on the upper and lateral surfaces with coarse chestnut-coloured hairs; on the ventral aspect the hairs are dark brown in colour. About the middle of its length it is covered with coarse black hairs, which increase in length distally on the upper and under surface until, especially on the upper surface, they form a distinct black crest, a smaller crest being present on the under surface. The tail is considerably swollen out proximally and somewhat incrassated, though the incrassation is hidden by the body hairs, which pass on to the root of the tail. Ear when laid forward reaching to the posterior border of the eye. They are covered internally and externally with short, stiff hairs. The eye is surrounded by a light ring of hairs. Hairs on the fold of the pouch and in the pouch-area, where they are scanty, are white, hands and feet white or light grey above. Palms with six granulated elevations, each with a small unstriated pad. There is a small tuft of white, whisker-like hairs on the posterior side of the fore-arm just above the wrist. Soles of feet with three granulated elevations at the base of the toes, each with a small unstriated pad. The soles are hairy in the heel region and have a series of thick-set, strong hairs running along the outer and inner margins and bending over on to the under surface, only the median part of which, so far back as the heel, is really naked. The median part is strongly granulated. Pouch opening vertically downwards, with moderately-developed lateral folds. Mammae eight (may be reduced to six or rarely four)".



During the years 1920–25 the present writer received numerous living specimens from Mr. A. G. Bolam of Ooldea on the Transcontinental Railway, and in 1923 published an extended description of the external characters. This description rectified some of the omissions and ambiguities of Spencer's account and may be recapitulated as follows : " A sturdily built, short-limbed, compact little animal. The head is somewhat flat and the muzzle is more blunted than in most of its allies (see fig. 1). The coat is fine and soft, mostly consisting of under-fur, which on the dorsal surface is slate grey at the base and bright brown at the tips. General colour varying from soft buff to bright red-brown, becoming warmer and brighter upon the back. Hairs of the mid-dorsal region measuring 10 mm. Face light

Fig. 1.



Adult female from Ooldea. Two-thirds natural size.

brown, brighter round the eyes, and along the upper lip. Outer side of limbs sandy coloured. Chin, throat, ventral surface of the body and inner side of the limbs creamy white or pure white. Manus and pes white. Tail shorter than the head and body ; it is thickened, the thickening starting almost at the base and extending for some two-thirds of the total length of the tail. Root of the tail clothed by a continuation of the red-brown body hairs. Immediately following this basal portion of the tail, the proximal, and swollen, portion is clothed by short, closely adpressed hair of a bright fox red colour. The terminal tapering half of the tail is ornamented with a large dorsal and a small ventral crest of shining black hairs. The ventral crest is inconspicuous and consists of short stiff

hairs that do not increase in length as they are followed towards the tip of the tail. The dorsal crest consists of long hairs which, starting as a mere ridge of fine black hairs, increases in length towards the tip of the tail and constitutes a fine fin-like crest.

The ears stand well away from the head and are rounded in outline. In colour they are slightly paler than the general body tint. The outer surface is clothed by fine creamy or sandy hairs. When the ear is laid forward it fails to reach the posterior angle of the eye. There is a single processus antihelicis (see fig. 2).

The muzzle is not so pointed as in the other Pouched Mice. The naked rhinarium is finely tessellated in texture and pale brown in colour. It is deeply cleft in the mid line, the cleft being continued to the upper lip and to the dorsal surface of the naked area (Pl. II, fig. 3). The nostril is cleft laterally.

The eye is surrounded by a pale area of hair. The eyelashes are dark, and better developed upon the upper than upon the lower lid. The eye is black and rather large.

Fig. 2.

Head of an adult female.  $\times 2$ .

There are four rows of mystacial vibrissae (see fig. 6): the individual hairs are black but, when elongated, the tip is pale; the longest measure 33 mm. The supraorbital set contains only one or two short dark bristles. From four to six long pale vibrissae spring from the genal tubercle. The submental set is represented by a few pale hairs and three long white vibrissae spring from the interramal papilla. The ulnar carpal vibrissae are well marked and two long (18 mm.) and two short bristles are present.

The palm of the manus is naked, granular and almost white in colour. There are five well-developed pads and a sixth (proximo-radial) less distinct. The pads are granular. Each pad has a central specialised granule (not so well marked in the proximo-radial pad) which marks the contact point of the pad, and which is surrounded by the smaller uniform granulations of the palm. The central granules are plain; there being no striations or punctures upon them. The



digital formula is  $3>4>2>5>1$ ; digits 2 and 4 being almost equal. Apical pads are present on the digits and they are unstriated (see fig. 3).

The soles of the feet are naked in the anterior portion and hairy towards the heel. The naked portion is granular. There are three well-developed pads. Each pad is granular; but, as in the palm, there is a definite central area marked out on the pad; in the sole this central area is sculptured by fine transverse striae. This species has always been described as being distinguished by having unstriated pads, but no specimen that I have examined has failed to show the presence of some definite striations on the pads of the sole (see fig. 4). The digital formula is  $4>3>5>2>1$ ; digits 3 and 5 being almost equal. The hallux is

Fig. 3.

Palmar aspect of left manus.  $\times 4$ .

small, but remarkably variable in its degree of development, and it possesses no claw. Apical pads are unstriated. The pouch in the quiescent state is practically obsolete. Nipples from 6 to 8".

The hair tracts are of basal simplicity (see fig. 5), there being no whorls or reversals anywhere on the body.

It is to be noted that this account departs most conspicuously from that of Spencer in describing the plantar pads as being striated, whereas according to that author they are, like the palmar pads, "unstriated". The striations are fine and linear but are easily recognized in all young and young adult specimens, though often being obscured by wearing in old individuals. This detail is of some importance, since in *Sminthopsis* the pads on both manus and pes are unstriated, while

Fig. 4.



Plantar aspect of left pes.  $\times 4$ .

Fig. 5.

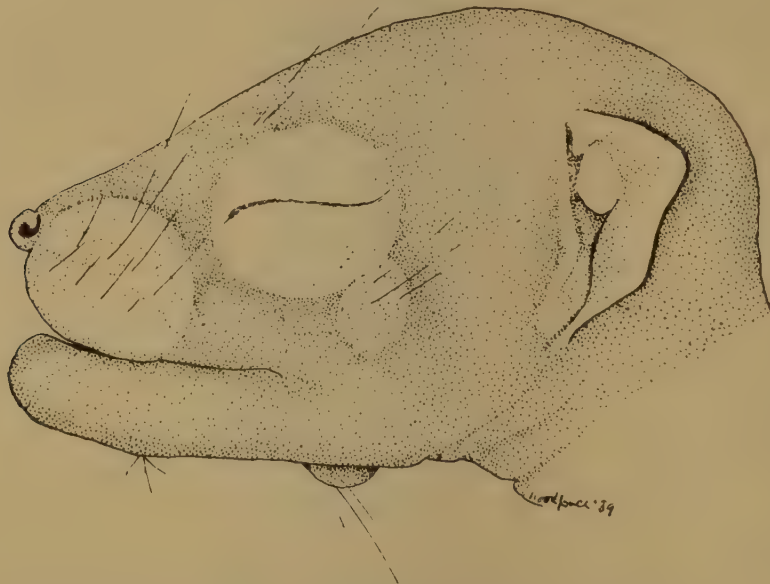


Hair tracts of a male pouch embryo 25 mm. R. V. length.



in *Phascogale* the striations are well developed and occupy the whole central area of the pads on both manus and pes. In *Dasyurus* (sens. lat.) the condition of the pads is variable, while in *Dasyuroides* Pocock describes the palmar pads as "very finely striolate", his description being almost certainly taken from Spencer's account, but this feature is not mentioned by Carlsson (Pocock, R. I., *Proc. Zool. Soc. Lond.*, 1926, pp. 1037-1084; Carlsson, A, *Acta Zoologica*, 7, pp. 249-275, 1926). The plantar pads of *Dasyuroides* are, however, said by Pocock to be smooth, a condition the exact reverse of that seen in *Dasyercus* and definitely contradicted by Spencer's original account of *Dasyuroides* in which he describes "fairly well-marked striations".

Fig. 6.



Characters of the head of a pouch embryo 30 mm. R. V. length.  $\times 6$ .

#### THE QUESTION OF ALLIED SPECIES

It would seem that, until far more extensive collections of the smaller members of the mammalian fauna of the arid central area are available for study, it is best to regard the species *cristicauda* as the only member of the genus.

In 1904 Waite (*Rec. Aust. Mus.*, 5, 123, Jan. 28) described some specimens of a "pouched mouse" received from Pilbarra, Western Australia. His description is as follows:

"*Phascogale blythi*, sp. nov. Size large, form delicate, fur close and soft with longer scattered hairs. The colour of the upper parts is sandy, speckled with brown, the basal portion of the fur being dark-grey; top of snout pale yellow, eye surrounded by a ring of light hairs, upper whiskers black, the lower ones white.

The whole of the under parts, together with the inner side of the limbs and the lining of the pouch is pure white. No grey at the base of the fur: the fore limbs are pale yellow above, the hands thinly clothed above with white hairs. Palms with granulated pads each with a raised striated area. Outside of thighs coloured

like the body above : upper side of feet thickly covered with white hairs, the under surface, the heel excepted, is naked but partly concealed by the hairs on the sides, which are bent underneath. There are three pads, striated and similar to those on the palms, and a small hallux which does not nearly reach the pads, it has no pad and is clawless. Tail of moderate length, shorter than the body, incrassated ; the proximal two-fifths above covered with short stiff yellow hairs, the remainder with gradually lengthening black hairs, *which do not however form a crest*. The whole of the lower surface is black, with the exception of a small proximal portion, which is yellow.

*Dimensions.*

	Male ad.	Female juv.
Head and body . . . . .	150	132
Hind foot . . . . .	27.8	26.5
Tail . . . . .	102	95

*Skull*.—Short and broad, the bones of the nasal region so thin as to enable the tooth roots to be seen through them ; muzzle short and broad, its lateral profile swollen by the roots of the canines which render its breadth more than one-third the basal length. Nasals rather long and noticeably expanded behind, their greatest breadth being more than one and a half times their least breadth. Interorbital space moderate, its edges at the constriction rounded, in front of which they are acute and form two prominences on each side, a larger long posterior one and a small tooth-like anterior one. Anterior palatine foramen extending to between the canines. Posterior palate with a pair of large vacuities opposite  $M^2$  and  $M^3$  and a pair of minute ones behind them. Bullae large and evenly rounded, their mastoid portion much swollen.

*Teeth*.—Of the upper incisors, the first pair are cylindrical, curved and separated from each other and from the second incisors, which are smallest. The lateral incisors are flattened, subequal in height, but graduated in length, the posterior ones being longest ; they are well separated from the canines which are long and slender.  $P^4$  not developed,  $P^3$  slightly larger than  $P^1$ . Lower incisors as large as the upper ones, spatulate, the anterior pair larger than the others. Canine without posterior basal ledge.  $P_1$  and  $P_3$  large, subequal, touching each other, in contact with the canine and  $M_1$  respectively.  $M_1$  narrowed in front without antero-internal secondary cusp.

*Dimensions.*

	Male ad.	Female juv.
Basal length . . . . .	35	33
Breadth . . . . .	24.1	22.9
Nasals, length . . .	12.2	10.7
Palate, length . . .	18	17.9
$M^1$ – $M^3$ . . . . .	8.2	8

This species is included by Iredale and Troughton (*Aust. Mus. Memoir*, 6, p. 8, 1934) in the genus *Dasyercus*, but since the animal appears to have had a well-developed pouch, striated pads on the manus and an uncrested tail, it would seem to be debarred from this generic title. When Waite was in charge of the Adelaide Museum he became acquainted with *Dasyercus cristicauda* but he never suggested



that my numerous specimens were in any way akin to the Western Australian form he had described previously. Unless a thorough re-examination of the type specimen is undertaken, it is best to omit the Pilbarra pouched mouse from the genus *Dasyercus*.

In 1905, Oldfield Thomas described a second species of the genus *Dasyercus*—*D. hillieri* :

This species was described from a single skin (without skull) from Killalpaninna : it was named after its discoverer, Mr. H. J. Hillier, an authority on the Aranda natives. The specimen differs from *C. cristicauda* only in being considerably paler in colour. It must be pointed out, however, that in intensity of coloration *C. cristicauda* is a very variable animal, and specimens that are considerably lighter than usual are often captured with the more normally coloured individuals.

*Dimensions of the type specimen (♂).*

Head and body . . . . .	150
Tail . . . . .	100
Hind foot . . . . .	30
Ear . . . . .	27

Unless further specimens from Cooper's Creek should show this type to be constant, with perhaps some cranial distinctions, it is best to regard it as merely a pale variety of the older species. By Iredale and Troughton (*op. cit.*) *hillieri* is regarded as a synonym of *cristicauda* and as such it is treated here.

In 1909, Shortridge (*Proc. Zool. Soc. Lond.*, 1909, p. 840) made reference to "*Phascogale blighi* Woodward" from Pilbarra. It is impossible to determine to what species his account applies and Iredale and Troughton are followed in regarding the name as invalid.

To the natives at Charlotte Waters *Dasyercus* is known by the name AMPERTA : at Ooldea Soak the native name is MULGARA.

#### HABITS, LIFE HISTORY AND ECOLOGY.

*Dasyercus* is a typical member of the Central Australian (or Eremian) desert fauna, inhabiting the great area beyond the 10-inch rainfall boundary. Both at Charlotte Waters and at Ooldea it shares its territory with the much rarer *Dasyuroides byrnei*, which it resembles in a striking manner. Both animals are well known to the natives and Spencer has recorded the fact that the Charlotte Waters natives insisted that *Dasyuroides byrnei* was the male of *Dasyercus cristicauda*. I do not know if the natives at Ooldea share this belief ; but, as Spencer noted, it is true that the males of the larger species are more often captured than the females, whereas with the other species the reverse is true. It is also a curious fact that *Dasyercus* may even exceed *Dasyuroides* in size, though as a rule it is a somewhat smaller animal. It is one of the most noteworthy features of *Dasyercus* (and this is evinced in some degree in several species from the Centre) that the size of the adult is subject to very wide variations, and it is a general rule that specimens bred in captivity in Adelaide tended to be larger than their parents captured in Ooldea. It is not only in general size that a wide degree of variability is shown, for the actual proportions of the different parts of the body manifest a

strange variability in different individuals. In the following table of measurements, the first 18 individuals are Spencer's specimens from Charlotte Waters and the last 12 are specimens from Ooldea; it is to be noted that the method of measuring the ear is different in the two series, Spencer's measurements not being in accordance with modern methods. In connection with this remarkable variation in the size of adult animals it is noteworthy that in the skeleton of one female which, captured as an adult and after producing three litters of young in captivity, might be regarded as relatively aged, the epiphyseal lines of the limb bones are unobliterated.

Specimen and sex.	Head and body.	Tail.	Hind foot.	Ear.
1 ♂	220	126	35	18
2 ♀	170	98	30.5	16
3 ♀	168	110	30.5	17
4 ♂	148	89	26	15.5
5 ♂	144	93	28	15
6 ♀	138	86	25	13.5
7 ♂	136	83	27	14
8 ♀	135	86	26	15
9 ♀	135	88	26	18
10 ♀	135	84	27	17
11 ♀	132	85	25	14.7
12 ♀	130	85	28	15.5
13 ♀	130	85	26	14
14 ♀	130	86	26	15
15 ♀	128	89	27	14.5
16 ♀	125	93	26	14
17 ♂ not adult	91	67	22.5	15
18 ♀ " "	86	51	20	12
19 ♂	180	92	31	25
20 ♂	180	80	27	21
21 ♂	180	82	27	20
22 ♂	170	102	30	24
23 ♂	170	85	28	20
24 ♀ with 7 embryos	160	93	26	20
25 ♂	160	84	27	18
26 ♂	155	100	29	23
27 ♀	155	75	25	18
28 ♀ with 7 embryos	150	84	27	20.5
29 ♀	130	82	23	28
30 ♂ adult	125	74	24	15

From this table it is seen that the head and body length may vary in adults from 220 to 125 and the hind foot may vary from 35 to 23: moreover, but little correlation is shown in these measurements, for whereas the hind-foot lengths of Nos. 5, 12 and 23 are identical (28 mm.), the head and body lengths of these individuals are respectively 144, 130 and 170, while their tail measurements are 93, 85 and 85.

Like all the small carnivores of the Central area, *Dasycercus* is an animal that is present, under normal conditions, in exceedingly small numbers, and were it not



for the knowledge of the native and his skill in tracking and capturing the small desert animals, specimens would be very difficult to come by. It suffers from the usual seasonal fluctuations that are typical of the semi-arid area and, at times, after a succession of bad seasons apparently disappears in consequence of its reduced numbers. In a good season, however, the animal responds quickly to the improved conditions and its numbers undergo a rapid increase : moreover, in good seasons it attains to an average larger size at maturity. It is, however, only during the periodic mouse plagues that visit the Central areas (such as those of 1903-05, 1911, 1916-17 and 1919-20) that it is seen in at all large numbers. On these occasions *Dasycercus* has been noted to increase with remarkable rapidity, and although no human ingenuity could check the increase of the mice, the appearance of these active little carnivores cleared them from certain districts (such as Clayton Creek) in a very short time. It normally lives in small burrows scratched out in sandhills but it is an animal of the open blue-bush, salt-bush and mulga sandhill country, and the burrow is more a breeding retreat than a permanent home. *Dasycercus* is without doubt one of the most intelligent of all the marsupials and it has all the curiosity and complete fearlessness of the smaller Eutherian carnivores. Those that I have had and bred in captivity have shown the most trusting boldness : they will come confidently to the hand, and although for their size one of the most efficient killing mechanisms among the carnivorous forms, they make no attempt to bite unless molested. They will thrust their noses against the wire of their run right into a cat's face, and this through no stupidity on their part, for both by vision and by scent they are perpetually well informed of their surroundings. Their auditory acuity also appears to be of a high order. As predatory animals, their development seems to be perfect, for quite a small animal will kill a starling with lightning precision, and they are equally proficient in capturing and killing grasshoppers and beetles. A large and active mouse introduced into the presence of a *Dasycercus* is killed in a flash if the animal is hungry : but if its appetite is appeased it will freely allow the mouse to occupy its bed in perfect amity until such time as it requires a meal. I have never known one to attack when it was not hungry. When hungry, its methods of mouse hunting are remarkable. It stalks its victim with remarkable cunning and when within striking distance its behaviour is invariable. Regarding its prey for a second the whole animal becomes rigid, its tail quivers in true lizard fashion, and with a lightning stroke seizes the mouse across the back of the head and practically with the stroke the mouse is dead. It is impossible, in witnessing this action, not to be reminded of the actions of a lizard stalking and seizing its living prey on a sunlit wall. Despite cramped quarters and strangeness of surroundings I have never seen the animal bungle the business of killing : one rush, one stroke delivered in a flash, a bulldog hold and the thing is over. After this remarkable exhibition of precision in killing, the animal usually attends to its toilet before proceeding further ; for in all things it is a remarkably dainty and clean creature. The business of eating a mouse is carried out in a most deliberate and methodical manner. The start is always made at the tip of the nose. The skin is separated and turned back. The skull is crushed and the brain devoured, and the body is eaten from head to tail, often without any

laceration of the skin. A rat that had provided a meal for three hungry young animals was skinned as neatly as though a skilled taxidermist had been at work. No bones were left attached to the hands and feet, the skin was turned completely inside out and was practically perfect.

Although a mouse or bird is always killed in a lightning rush, considerable caution is displayed in dealing with unfamiliar beetles, and it is a remarkable thing that all insects that are not immediately recognized and killed by biting are taken into the hand before being transferred to the mouth. Most beetles are caught with the hand, and the utility of the manus for searching out and picking up insects is very strikingly reminiscent of the methods of animals very high up in the Monodelphian series. Although such bloodthirsty little animals, they do not quarrel or fight among themselves and they may be placed together in a cage regardless of sex or acquaintance. In this regard they resemble *Dasyurus*, but differ markedly from the Peramelidae and most of the herbivorous marsupials. They will not kill a weak or sickly fellow, nor will they devour its body when dead; but they vacate a nest in which a dying comrade is lying and do not molest it in any way. They appear to be extremely affectionate little animals and they are fond of lying in the sun, two or more together with their heads on each other's backs. They are by no means nocturnal or crepuscular, being lovers of the sunlight and having a true lizard-like habit of lying perfectly flat in the hot sunshine. When doing this it is not uncommon for the hind legs to be turned backwards against the sides of the tail—as in a museum skin—and the abdominal cavity is spread flat, very much after the manner of a sun-basking lizard. The degree of heat and the intensity of sunlight they delight in is very remarkable in a mammal, and particularly lizard-like are the rapid quivering of the tail and short sharp movements of the limbs as the animal exposes itself to the direct rays of the sun. Correlated with this sun-basking habit it is worthy of note that the membranes surrounding the genital glands are pigmented intensely black: the same phenomenon being manifested in the sun-basking lizards of the Centre of Australia. There is also something remarkably reptilian in the way their vitality can be suspended in cold and adversity and can be revived by warmth. Most of those that have lived long and have bred in captivity have been received, after the long journey from the Centre, in a condition that could fairly be described as "dead". All were cold and apparently completely lifeless after the long winter journey from Ooldea Soak; but these apparently dead animals proved easy to resuscitate by heat and artificial respiration.

The breeding period (at Ooldea) is from June to September in ordinary seasons, and seven may be taken as an average litter. The pouch is practically absent; but when the young are very small they are more or less protected by a shallow ridge of integument bordering the pouch area. When the young have grown larger they depend from the mother's nipples unprotected by any skin fold of her ventral surface. (See Pl. I, fig. 1.) It is a very curious thing to see a mother, with seven large young depending from her nipples, staggering about in search of insects or in combat with mice. The time spent by the young clinging to the nipples is considerably over a month.



## OSTEOLOGY.

*The Skull.**Dimensions of skull.*

	Spencer.	Ooldea specimens (average.)
Basal length .....	34.5	35
Breadth .....	23.5	24
Nasals, length .....	12	12
Palate, length .....	18	18
M <sup>1</sup> -M <sup>3</sup> .....	7.5	8

The cranial characters of *Dasycercus* are perfectly distinctive and permit the generic features to be recognized without difficulty. From *Phascogale* it is readily diagnosed by the dentition, the characters of bulla and ectotympanic, and many other features. From *Dasyurus* and its subgenera the failure to develop an exoccipital (paroccipital) process, as well as the dentition and the ectotympanic, serve as reliable diagnostic criteria. From the point of view of cranial characters its nearest affinities are with *Dasyuroides*, in which also the paroccipital process is lacking.

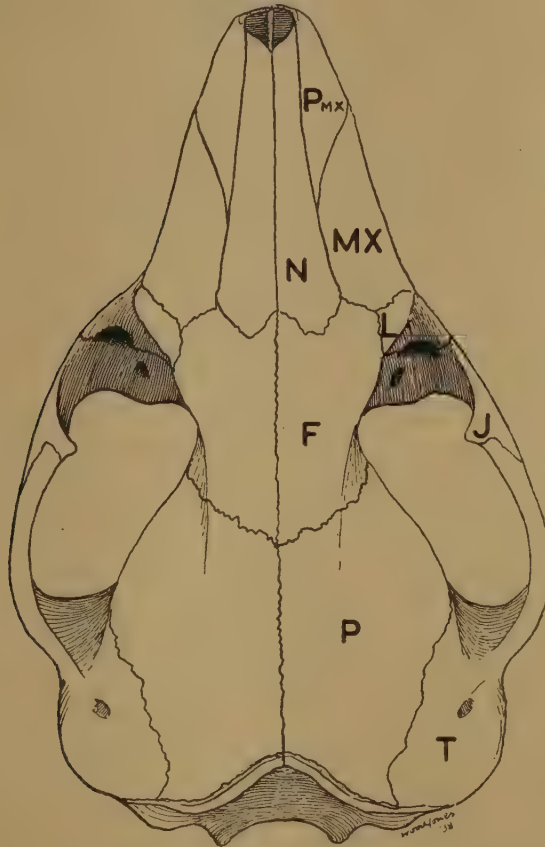
The skull is characteristically flat, the interorbital constriction only moderately marked when comparison is made with other members of its phylum, and the cranium is enlarged and rounded and but little ridged. From the lateral and basal aspects the enormously inflated bullae are the most conspicuous features. The cranial sutures, including those of the base of the skull, remain unclosed in animals that have produced more than one litter of young (see fig. 7).

The *Nasals* are expanded at their hinder end: the total maximum breadth of the two bones being a little less than half their total length. There is some individual variation in this ratio, some specimens having nasal bones the length of which is less than twice the total breadth, and in all cases a marked contrast is shown with *Dasyurus* and *Phascogale* in which the nasals are considerably more elongated. The likeness in this feature is with *Myrmecobius*, in which the length of the nasals is less than twice their total breadth. The form of the posterior ends of the nasals varies considerably. In some specimens the greatest length is at the mid line and in others it is nearer to the lateral margin of the individual bones. The articulation between the nasals and the frontals may therefore be almost transverse or it may be convex forwards or backwards at the middle line. There is often a considerable degree of asymmetry at the naso-frontal articulation, either the right (most commonly) or the left bone extending further back on the skull.

The *Frontals*, in young skulls, are evenly convex on the dorsum of the skull in front of the interorbital constriction; in older skulls this surface tends to be flattened, or even concave, towards the middle line. With this increasing flattening in older skulls the supraorbital margins become sharper and more defined. In young specimens the tapering to the interorbital constriction is even and gradual; in older specimens it tends to become more abrupt and to be notched behind a

supraorbital process. With this increasing notching of the supraorbital margin with advancing age, the temporal ridges on the hinder parts of the frontals become more marked. The form of the fronto-parietal suture is subject to wide individual variation: in some specimens it runs almost transversely across the skull, in others it runs from the mid line somewhat acutely downwards and forwards. There is commonly a considerable degree of asymmetry on the two sides of the skull. There is an excessive degree of overlap of the frontal by the parietal at the fronto-parietal suture. This is a common didelphian feature that in *Dasyercus* is

Fig. 7.



Skull in norma verticalis (specimen 9.2.149).  $\times 3$ . Pmx=premaxilla. MX=maxilla. N=nasal. L=lacrimal. F=frontal. J=jugal. P=parietal. T=temporal.

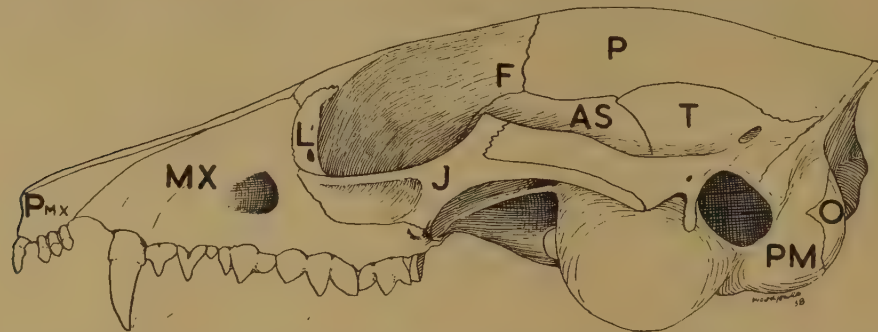
developed to an unusual degree. In a specimen in which the combined lengths of the frontal and parietal was 22 mm. the overlap of the parietal was slightly more than 3 mm.

The *Parietals* are evenly rounded with the contour of the cranium and are unridged even in old male specimens. They are markedly broader in front than behind, a feature in which *Dasyercus* resembles *Myrmecobius*. Below, the parietals articulate with the alisphenoids in front and the squamous temporals behind: the area allotted to the squamous temporal being about twice that



articulating with the alisphenoid (see fig. 8). The parieto-occipital suture is situated just in front of the occipital crest at the posterior end of the cranium.

Fig. 8.



Skull in norma lateralis (specimen 9.2.149).  $\times 3$ . PMX=premaxilla. MX=maxilla. L=lacrimal. J=jugal. F=frontal. AS=alisphenoid. P=parietal. T=temporal. O=occipital. PM=petromastoid.

The *Occipital* constitutes the posterior end of the cranial cavity, enters into the formation of the bulla and passes forwards on the base of the skull to the occipito-sphenoid suture which remains patent even in the skulls of old specimens. In constituting a large element in the formation of the bulla, the exoccipital element of *Dasyercus* appears to be unique (see fig. 9). In *Phascogale* and *Dasyurus* the exoccipital passes behind the region of bulla inflation and terminates in the solid paroccipital process. In *Dasyercus* no paroccipital process is developed and the site from which it takes origin in normal forms is wholly occupied with the formation of the thin posterior wall of the bulla. Probably *Dasyuroides* presents a somewhat similar condition but the description of the bulla region by Carlsson is not clear on this point. The suture between the basioccipital and the exoccipital elements passes through the anterior fourth of the condyle. The foramen magnum is large and longer in its transverse than in its vertical axis. The basioccipital element is wide and flat, its breadth at the hinder margin being equal to its antero-posterior length in the mid line.

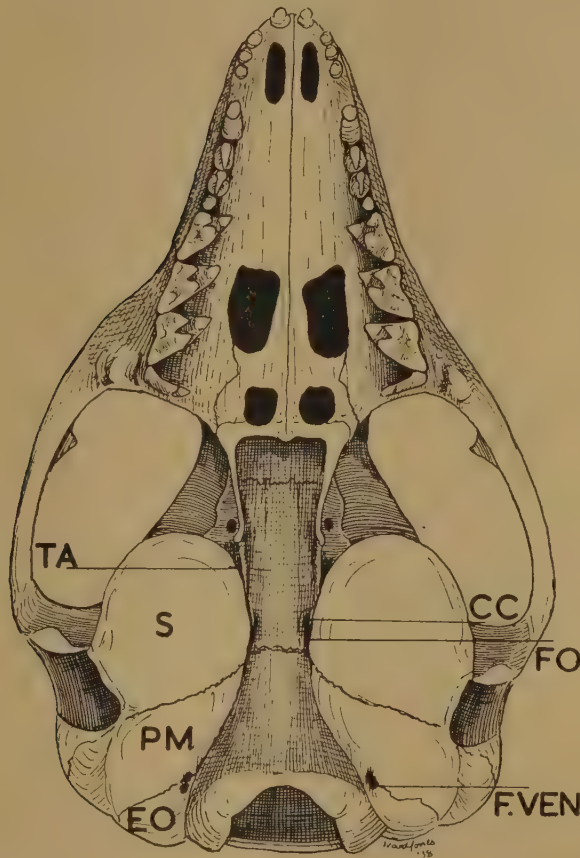
The *Premaxilla* is marked off from the maxilla by a suture that persists throughout life. This suture passes a full millimetre, or slightly more than the diameter of the canine, in front of the upper canine tooth and at this point the premaxilla is widely overlapped by the maxilla. The upper and posterior termination of the premaxilla extends between the maxilla and the nasal for a somewhat variable distance. In some specimens the articulating area of nasal and premaxilla is twice as long as that of nasal and maxilla: in others the two articulating areas are of nearly equal length.

The *Maxilla* articulates with the lacrimal on the facial aspect of the skull over an area that may be as long as 5 mm., the lower extremity of the lacrimomaxillary suture being below the upper level of the infraorbital foramen. In this feature *Dasyercus* approaches *Myrmecobius* and differs from *Dasyurus* and *Phascogale* in which an extension of the jugal intervenes between the maxilla and the lower portion of the lacrimal. The jugalmaxillary suture passes below (or through) the

zygomatic tubercle to the hinder end of the alveolar margin behind the last molar tooth, where the maxilla articulates with the palate.

The *Lacrima* appears both on the face and in the orbit. On the face it articulates with the frontal, maxilla and jugal. The foramen for the naso-lacrimal duct

Fig. 9.



Skull in norma basalis (specimen 9.2.149).  $\times 3$ . TA=Eustachian orifice. S=sphenoid. PM=petromastoid. EO=exoccipital. CC=carotid canal. FO=foramen ovale. F.VEN=venous foramen.

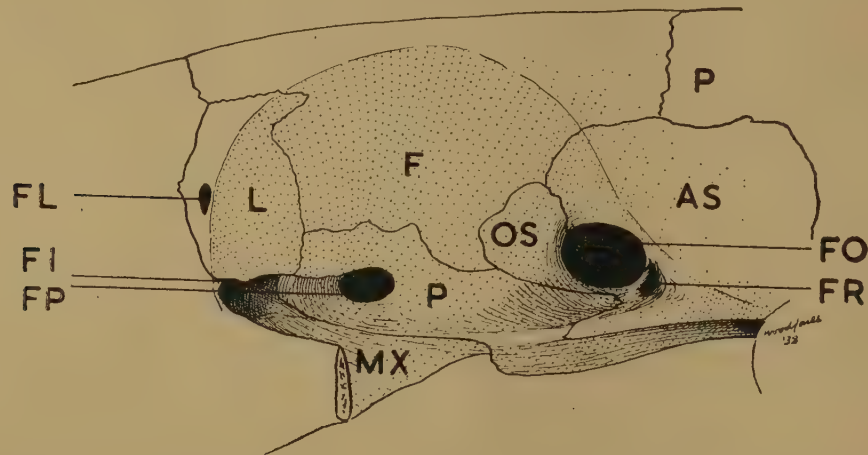
is situated just without the orbital margin and has to its medial side a vascular foramen that ultimately joins the canalis nasolacrimalis. In the orbit the fronto-lacrimal articulation is elongated and vertical; and, below the frontal, the lower border of the bone articulates with the palate. There is a free lower border arching over the entrance to the infraorbital canal and lateral to this the lacrimal articulates with the jugal, which overlaps it on its lateral aspect (see fig. 10).

The *Jugal* articulates anteriorly with the lacrimal and maxilla but does not extend so far on the face as is usual in *Dasyurus* and *Phascogale*, its anterior extremity being below the level of the foramen for the nasolacrimal duct. Behind, it extends back to enter into the temporomandibular articulation as it does in members of the allied genera. It gives rise to a well-marked postorbital process, in the formation of which the zygomatic process of the temporal takes no part.



The *Temporal* shows a squama situated relatively far back on the cranial wall in consequence of the great development of the alisphenoid. At the alisphenoid-temporal suture the alisphenoid is overlapped by the temporal above but overlaps the temporal below. At the squamous suture the temporal overlaps the parietal to a considerable extent. Both suture lines are extremely simple, the alisphenoid-temporal suture being concave forwards, herein differing from the condition usual in allied genera; and the squamous suture is, as usual, convex upwards. The lateral part of the squamous temporal, articulating with the mastoid, is inflated and forms part of the roof of the extra-tympanic portion of the bulla. Just in front of the inflated portion the temporal is pierced by a large venous foramen which communicates with the posterior end of the superior petrosal sinus. Both squamous temporal and alisphenoid contribute to the formation of the upper aspect of the root of the zygoma: but below, in the temporo-mandibular articulation,

Fig. 10.



Inner wall of left orbit (specimen 9.2.149).  $\times 6$ . FL=lacrimal foramen. FI=infraorbital foramen. FP=palatine foramen. L=lacrimal. F=frontal. P=palatine. MX=maxilla. OS=orbitosphenoid. AS=alisphenoid. P=parietal. FO=combined optic foramen. FR=foramen rotundum.

the alisphenoid is excluded. The petro-mastoid portion of the temporal is separate in the young adult skull, and its junction with the rest of the temporal and the exoccipital is distinct even in the skulls of old specimens. It passes obliquely downwards and forwards, articulating with the parietal by its apex, with the squamous temporal, the ectotympanic and the sphenoid in front and with the exoccipital and basioccipital behind and below. In its lower part it shares with the sphenoid and exoccipital the inflation of the auditory bulla.

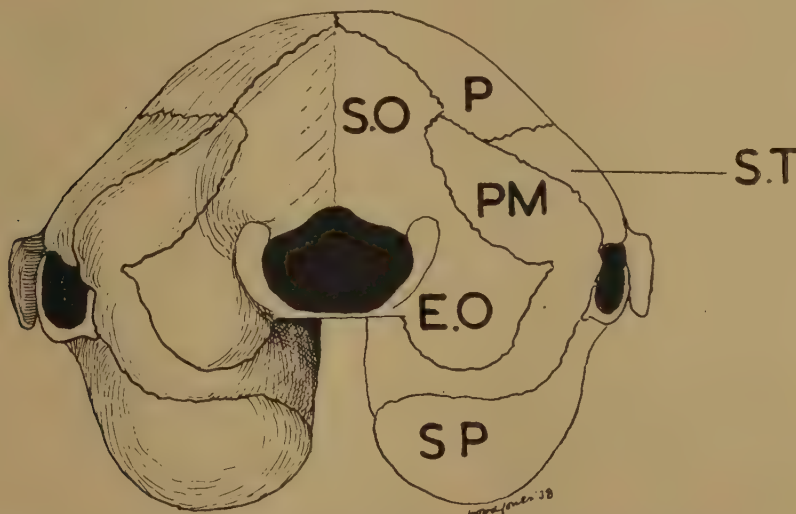
The *Sphenoid* is distinguished mainly by the large size of the alisphenoid element and the enormous contribution that is made to the formation of the bulla. The basisphenoid is considerably narrower than is the same element in *Dasyurus* or *Phascogale*. The medial pterygoid laminae are prolonged backwards to the site of the carotid foramen: the lateral plates are extended in a horizontal direction below the foramen rotundum. The orbitosphenoids are small, the wide gap made by the combined sphenoidal fissure and optic foramen extending almost to its

lower margin. The foramen rotundum, foramen ovale and carotid canal all pierce the sphenoid (see figs. 9, 17, 78 and 79).

The *inner wall of the orbito-temporal fossa* (see fig. 10). At the anterior limit of the fossa the posterior margin of the lacrimal articulates with the frontal above and the palate below and then arches over the posterior end of the infraorbital canal. Behind the lacrimal the frontal articulates with the palate below and with the orbitosphenoid and alisphenoid behind. The orbitosphenoid articulates at its lower margin with the upper edge of the palate. On the floor of the anterior portion of the fossa the lower margin of the palate articulates with the maxilla and just above the suture line the bone is pierced by the large naso-palatine canal.

The *Bulla* (see figs. 11-15) is perhaps the outstanding feature of the skull, since the inflation is so enormous that it occupies more than a third of the total basal length of the skull. From before backwards on the base of the skull three elements

Fig. 11



Norma occipitalis of the skull of a young specimen. SO=supraoccipital. EO=exoccipital. P=parietal. PM=petro-mastoid. ST=squamous temporal. SP=sphenoid.

are involved in the inflation. The sphenoid is by far the largest constituent, forming about two-thirds of the total expansion, the petro-mastoid (including an entotympanic element) makes the major contribution behind the external auditory meatus, and the exoccipital constitutes the extreme hind end. In addition, the squamous temporal forms the intermediate portion of the roof of the cavity and of the epitympanic recess. The ectotympanic (or rather, a lateral outgrowth from it) appears on the surface of the skull only at the anterior and inferior margins of the external auditory meatus. The interior of the bulla cavity is partially septate, for one flange exists between the portions constituted by the sphenoid and the petro-mastoid and another between the petro-mastoid portion and that derived from the exoccipital. These flanges exist as sculptured ridges encircling the girth of the bulla and causing only minor constriction of the cavity. Within the cavity formed by the sphenoid element is the ectotympanic with the membrana tympani



and the malleus. The ectotympanic thus situated deep within the bulla repeats the condition typical of the lemurine Lemurs : but the ectotympanic of *Dasycercus* differs from that of *Lemur* for, whereas in *Lemur* the ectotympanic and membrana tympani are brought into continuity with the bulla mouth by a fibrocartilaginous tube, in *Dasycercus* a bony tube passes from the ectotympanic and membrana to the "external auditory meatus". The condition is a very remarkable one, for an ectotympanic external auditory meatus is formed within the bulla cavity and re-establishes continuity with the external air by growing to the bulla mouth and

Fig. 12.

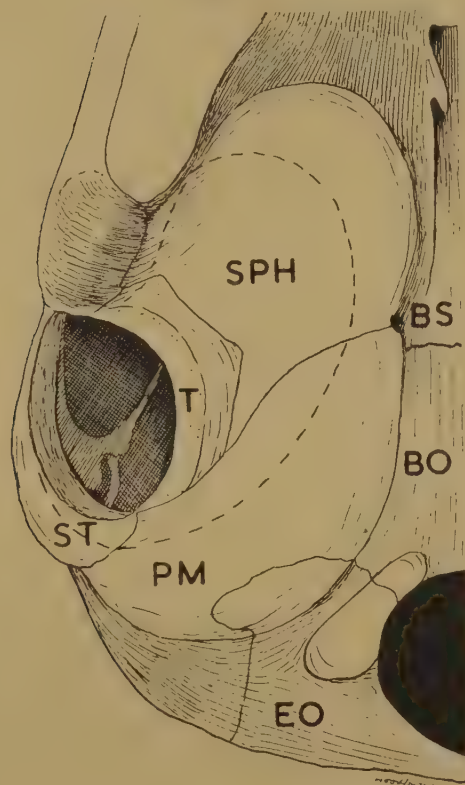


Fig. 13.

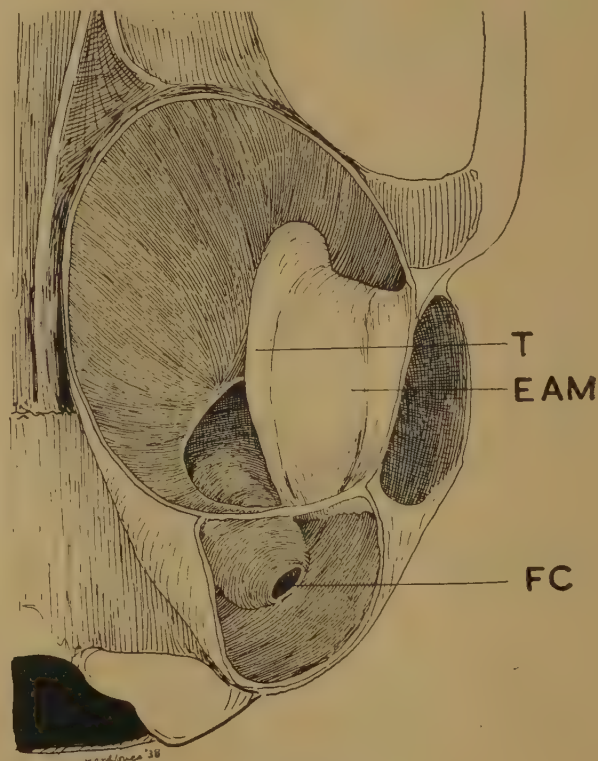


Fig. 12.—Right bulla region of a suckling young.  $\times 8$ . SPH=sphenoid. T=tympanic. ST=squamous temporal. PM=petro-mastoid. BS=basisphenoid. BO=basioccipital. EO=exoccipital.

Fig. 13.—Left bulla of an adult opened from below.  $\times 6$ . T=tympanic. EAM=external auditory meatus. FC=fenestra cochleae.

forming a portion of the bulla mouth on its anterior and inferior aspects. The posterior and superior portions of the ectotympanic (less than a third of its total circumference) are fixed to the temporal bone : but the fixation is effected only by the cornuate extremities of the incomplete annulus. In the whole of the remainder of its circumference the ectotympanic is entirely free within the bulla cavity. Within that part of the bulla derived from the petro-mastoid and fused entotympanic is the conspicuous swelling of the promontory and, at its posterior end, the large fenestra cochleae. The smaller fenestra vestibuli opens just above the posterior end of the promontory. The epitympanic recess, formed in the squamous temporal, communicates with the bulla cavity above the head of the malleus.

The contribution to the bulla made by the exoccipitals is very considerable and is all the more remarkable since it does not occur in allied genera and is not mentioned by Carlsson even in *Dasyuroides* in which, since this animal also fails to develop a paroccipital process, it would be expected to be present. The Eustachian tube opens upon the mesial wall of the bulla just behind the flange which marks the contribution from sphenoid and petro-mastoid elements, and at its anterior end opens immediately posterior to the foramen for the third division of the Vth

Fig. 14.

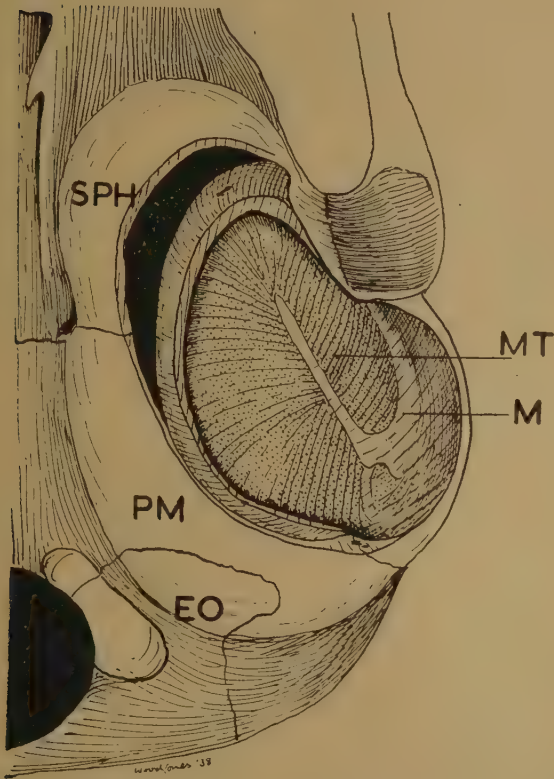


Fig. 15.

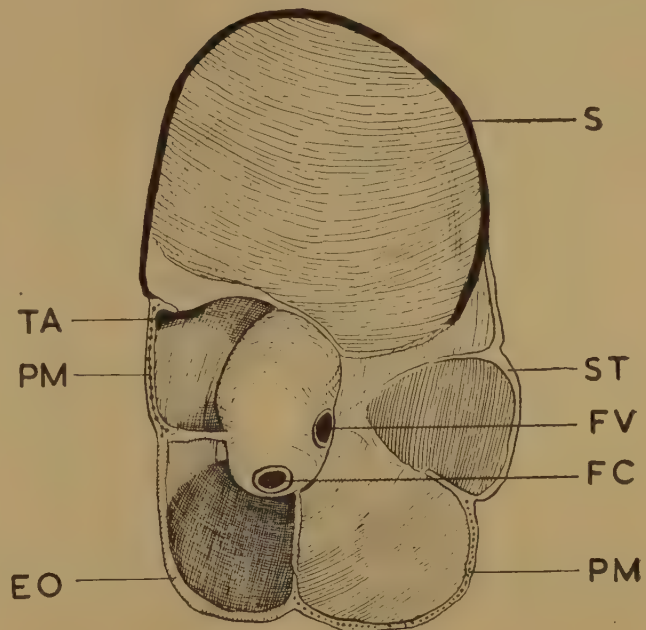


Fig. 14.—Left bulla of a suckling young opened from below.  $\times 8$ . SPH=sphenoid. PM=petro-mastoid. EO=exoccipital. MT=membrana tympani. M=malleus.

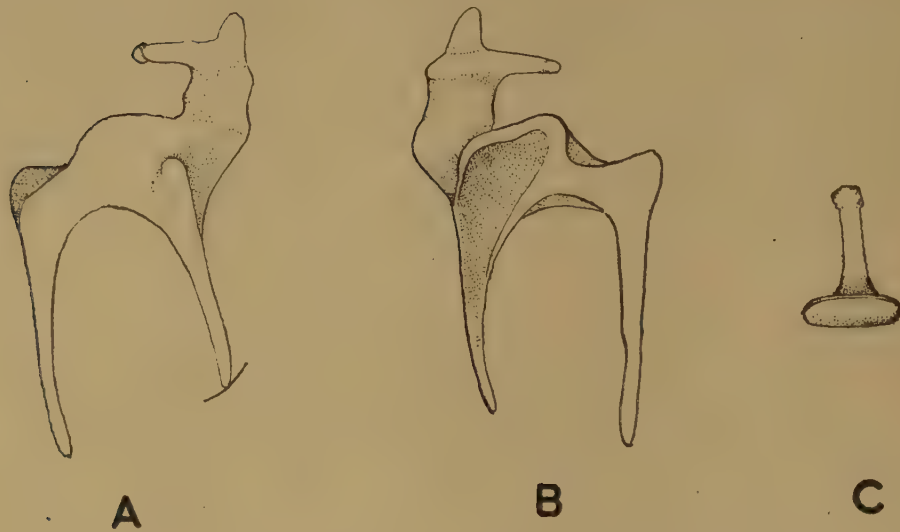
Fig. 15.—Diagram of the major constituent parts of the left bulla. TA=Eustachian orifice. PM=petro-mastoid. EO=exoccipital. S=sphenoid. ST=squamous temporal. FV=fenestra vestibuli. FC=fenestra cochleae.

nerve and medial to the entrance of the carotid canal.

The *auditory ossicles* display certain of the general characters of these bones characteristic of the Didelphia but in details of form show some rather striking peculiarities (see fig. 16). The malleus and incus are ankylosed even in the suckling animal and the whole compound bone is strikingly smaller in the young animal than it is in the adult. The compound bone possesses two long processes, the one terminating at a free extremity in the membrana tympani, the other passing forwards across the membrana to impinge on the annulus. The incus likewise possesses two processes, a short stout rounded boss being its proper articular facet and a more elongated process which meets the apex of the rod of the stapes. The stapes itself is extremely simple, being shaped like a minute collar-stud.

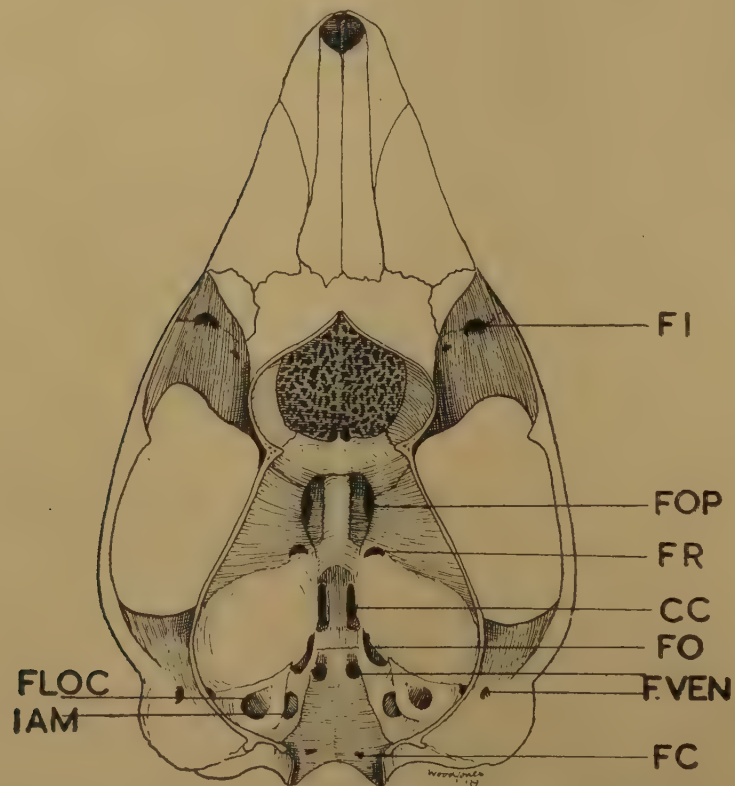


Fig. 16.



Ossicles of the right ear. A. Compound malleus-incus, lateral aspect.  
B. The same, medial aspect. C. Stapes.

Fig. 17.



Endocranial aspect of base of skull.  $\times 3$ . FLOCC=floccular fossa. IAM=internal auditory meatus.  
FI=infraorbital foramen. FOP=combined optic foramen. FR=foramen rotundum.  
CC=carotid canal. FO=foramen ovale. F.VEN=venous foramen. FC=condyloid  
foramen.

The foot piece is almost circular and the remainder of the bone consists of a simple columella, the apex of which is articulated with the long process of the incus.

The *endocranial* aspect of the cranial base shows, on the floor of the cranial cavity anterior to the interorbital constriction, the enormously enlarged cribriform plate of the ethmoid, separated from the presphenoid behind by a well-marked suture (see fig. 17). The frontal bones constitute only the side walls of the anterior part of the cranial cavity and make no contribution to its floor, which is constituted solely by the ethmoid. The anterior part of the cranial cavity, behind the interorbital constriction, is composed of the sphenoid and is sharply divided into an anterior concave portion and a posterior convexity where the bulla inflation of the sphenoid trespasses into the cranial cavity. The combined optic and sphenoidal foramina are situated at the junctions of orbito-, ali- and basi-sphenoid elements and the foramen for the second division of the Vth nerve pierces the alisphenoids immediately in front of the bulla inflation. The basi-sphenoids are pierced near the mid line, immediately to the inner side of the inflated area, by the cranial emergence of the carotid canals. The foramen for the third division of the Vth nerve is situated between the junction of the hinder part of the alisphenoid and the apex of the petrous. The basioccipital transmits the foramen lacerum posterior at its junction with the petrous and nearer to the foramen magnum is perforated by the anterior condylar foramina. The upper surface of the petrous is hollowed by a large floccular fossa and below and medial to this is situated the internal auditory meatus. Between the petrous and the sphenoid elements of the roof of the bulla is the large venous foramen which emerges from the skull upon the outer surface of the squamous temporal at the upper root of the zygoma.

DENTITION. See figs. 8, 18 and 19.

The account of the dentition as given by Oldfield Thomas, who relied on Krefft's original description (no specimen being available to Thomas), is as follows :

“ Upper P<sup>4</sup> minute, tubercular.

Lower I<sub>1</sub> larger than I<sub>2</sub> and I<sub>3</sub>.

Canine slender, not broadened posteriorly at its base.

Lower P<sup>4</sup> wholly absent.

M<sup>1</sup> with scarcely an indication of the anterior secondary cusp ”.

Baldwin Spencer elaborated this from the examination of material collected by the Horn Expedition. By him the dental formula is given as follows :

I.4. C.1. PM.3. M.4.

I.3. C.1. PM.3. M.4.

and the special features are noted as follows :

“ In the upper jaw the first incisor is larger than the other three, and is separated from them by a diastema. The canine is large and strong and measures 3 mm., or even slightly more in length. P<sup>3</sup> is larger than P<sup>1</sup> and P<sup>4</sup>, if present at all, is minute, tubercular and usually absent. In the lower jaw the three incisors of each side are sub-equal, close together and to the canine, which is strong and measures 2.5 mm. in height. P<sub>4</sub> is quite wanting, and P<sub>3</sub> often lies close against M<sub>1</sub> or is separated from it by a slight diastema ”.



One of the most interesting features of the dental formula is its comparison with those typical of presumably nearly allied genera.

The formula for *Dasyurus* (including *Dasyurus*, *Dasyurinus*, *Satanellus* and *Dasyurops*) is :

$$\begin{array}{cccc} \text{I.4.} & \text{C.1.} & \text{PM.2.} & \text{M.4.} \\ \hline \text{I.3.} & \text{C.1.} & \text{PM.2.} & \text{M.4.} \end{array}$$

That for *Phascogale* (including *Phascogale* and *Planigale*) is typically :

$$\begin{array}{cccc} \text{I.4.} & \text{C.1.} & \text{PM.3.} & \text{M.4.} \\ \hline \text{I.3.} & \text{C.1.} & \text{PM.3.} & \text{M.4.} \end{array}$$

For *Sminthopsis* it is the same, whereas for *Dasyuroides*

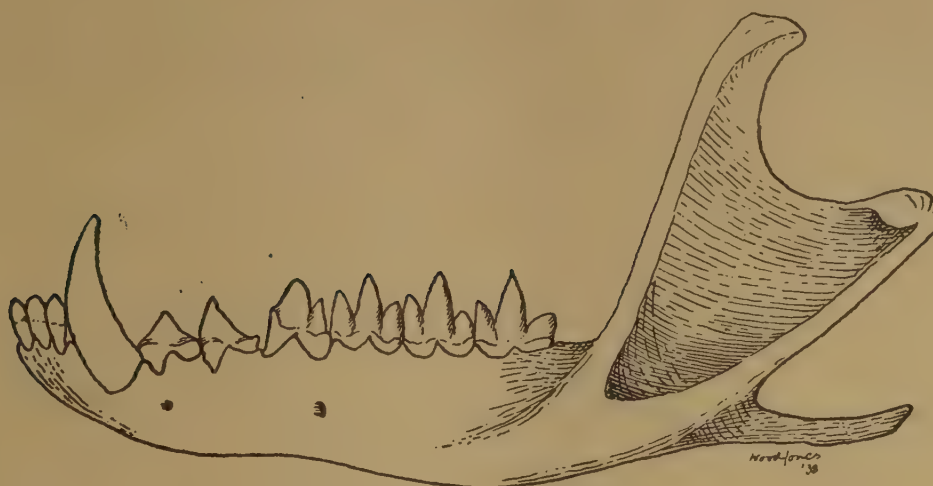
$$\begin{array}{cccc} \text{I.4.} & \text{C.1.} & \text{PM.3.} & \text{M.4.} \\ \hline \text{I.3.} & \text{C.1.} & \text{PM.2.} & \text{M.4.} \end{array} \quad \text{is usual in adults.}$$

It is obvious that *Dasyercus*, in the reduction of its premolar teeth, has approached to the condition typical of *Dasyurus*, the condition present being more frequently that of *Dasyurus* than that of *Dasyuroides*.

The following table records the numerical formulae of the skulls of adults :

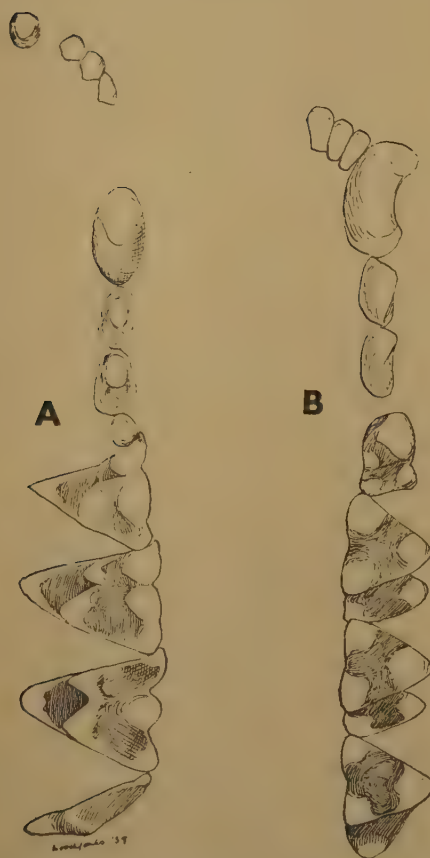
♂	9.2.149	$\begin{array}{cccc} \text{I.4.} & \text{C.1.} & \text{PM.3.} & \text{M.4.} \\ \hline \text{I.3.} & \text{C.1.} & \text{PM.2.} & \text{M.4.} \end{array}$
		Upper PM <sup>3</sup> minute.
♀	9.2.169	$\begin{array}{cccc} \text{I.4.} & \text{C.1.} & \text{PM.2.} & \text{M.4.} \\ \hline \text{I.3.} & \text{C.1.} & \text{PM.2.} & \text{M.4.} \end{array}$
		No trace of PM <sup>3</sup> . Teeth worn.
♀	9.2.166	$\begin{array}{cccc} \text{I.4.} & \text{C.1.} & \text{PM.2.R.} & \text{PM.3.L. M.4.} \\ \hline \text{I.3.} & \text{C.1.} & \text{PM.2.R.} & \text{PM.3.L. M.4.} \end{array}$
		On R. PM <sup>1</sup> minute. PM <sup>2</sup> normal. PM <sup>3</sup> absent.
		On L. PM <sup>1</sup> minute. PM <sup>2</sup> normal. PM <sup>3</sup> minute.
♀	9.2.168	$\begin{array}{cccc} \text{I.4.} & \text{C.1.} & \text{PM.3.R.} & \text{PM.2.L. M.4.} \\ \hline \text{I.3.} & \text{C.1.} & \text{PM.1.R.} & \text{PM.2.L. M.4.} \end{array}$
		No trace of PM <sup>1</sup> R.
♀	9.2.170	$\begin{array}{cccc} \text{I.4.} & \text{C.1.} & \text{PM.2.} & \text{M.4.} \\ \hline \text{I.3.} & \text{C.1.} & \text{PM.2.} & \text{M.4.} \end{array}$
		No trace of upper PM <sup>3</sup> .
♂	9.2.165	$\begin{array}{cccc} \text{I.4.} & \text{C.1.} & \text{PM.2.} & \text{M.4.} \\ \hline \text{I.3.} & \text{C.1.} & \text{PM.2.} & \text{M.4.} \end{array}$
		No trace of upper PM <sup>3</sup>
♂	9.2.167	$\begin{array}{cccc} \text{I.4.} & \text{C.1.} & \text{PM.2.R.} & \text{PM.3.L. M.4.} \\ \hline \text{I.3.} & \text{C.1.} & \text{PM.2.} & \text{M.4.} \end{array}$
		PM <sup>3</sup> upper absent on the right side.
♂	9.2.17	$\begin{array}{cccc} \text{I.4.} & \text{C.1.} & \text{PM.3.} & \text{M.4.} \\ \hline \text{I.3.} & \text{C.1.} & \text{PM.2.} & \text{M.4.} \end{array}$
		PM <sup>3</sup> upper of both sides only visible with lens.

Fig. 18.



Mandible and mandibular teeth.  $\times 4$ .

Fig. 19.



A. Upper and B. Lower teeth. Occlusal surfaces.  $\times 6$ .

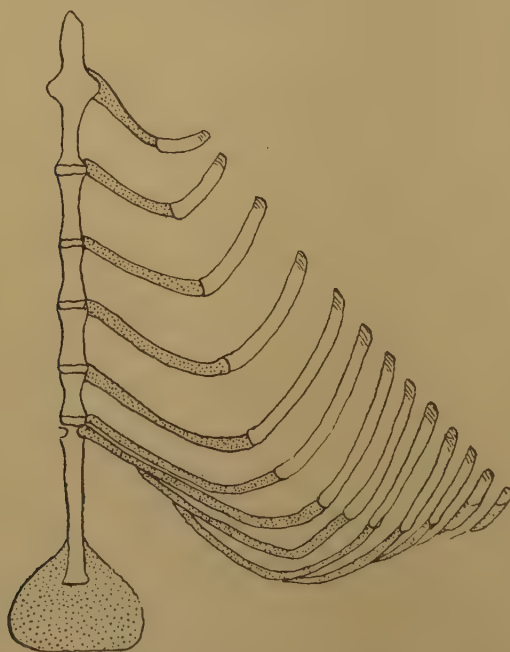


As to the form of the teeth, Spencer's description of the canine as "large and strong" is certainly more appropriate than Thomas's "slender", for relatively to the size of the skull, the canines are longer and stouter than those of *Dasyurus* or *Phascogale*. The upper central incisors are only slightly larger than the three laterals and although they are separated from them by a space, as in *Phascogale*, they do not project to the same extent as do the first incisors in members of that genus. The lower central incisors are considerably broader than the two laterals. When the last premolar is present in the upper jaw it consists of little more than a minute amorphous enamel tubercle. This is of course in marked contrast to *Phascogale* in which the posterior premolar is considerably larger than the two anterior to it. The third premolar in the lower jaw is absent in all specimens that I have examined and in all those recorded by Spencer as well as in the type specimen. The first lower molar resembles the corresponding tooth in *Dasyurus* but differs markedly from that of *Phascogale* in the almost complete absence of the anterior cusp. The first upper premolar is single rooted, the second has two roots. The three anterior molars possess three roots and the fourth, two roots. Both lower premolars and all the molars are two-rooted teeth.

#### APPENDICULAR SKELETON.

The *Sternum* (see fig. 20) consists of a pointed presternum expanded at the point at which the first rib effects its articulation. The mesosternum consists of four

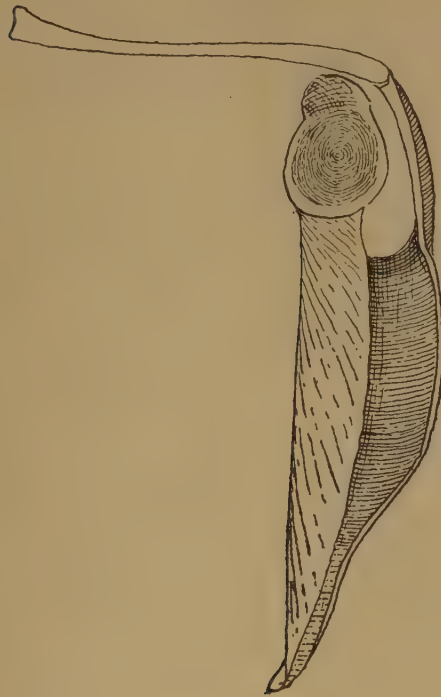
Fig. 20.



The sternum and ribs.  $\times 2$ .

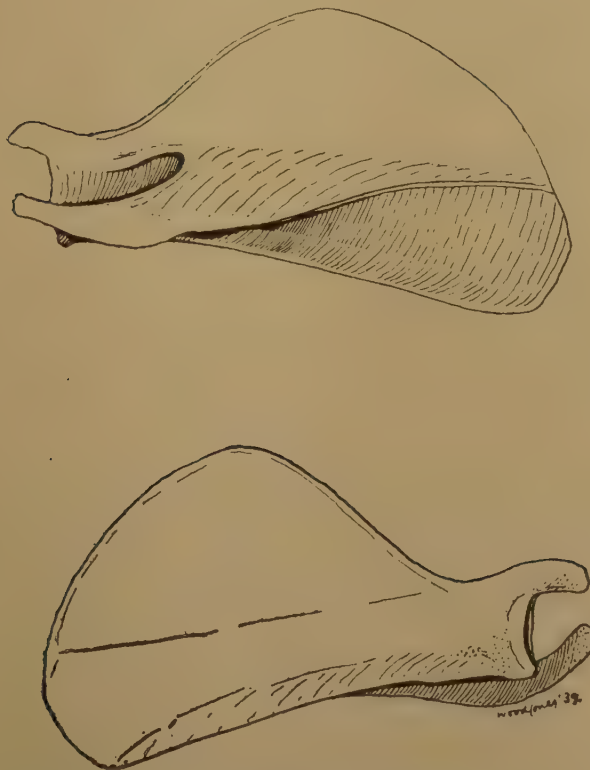
separate elements, expanded at their articular surfaces and narrowed at their mid points: the anterior elements being somewhat more slender than the posterior. The ziphisternum has a long styliiform ossified portion which expands posteriorly

Fig. 21.



Left clavicle and scapula. Ventral aspect.  $\times 4$ .

Fig. 22.



Left scapula. Dorsal and ventral aspects.  $\times 4$ .



into a broad leaf-like cartilaginous plate which, even in the adult, shows no trace of ossification.

The *Ribs* are thirteen in number. Of these the anterior seven articulate directly with the sternum. The articular extremity of the first is broad and, in fully adult specimens, the costal cartilage is largely ossified. The second, third, fourth, fifth and sixth articulate at the junctions of the respective sternebrae: the seventh articulates with the ventral surface of the upper extremity of the ziphisternum, just below its articulation with the last element of the mesosternum. The eighth, ninth, tenth and eleventh costal cartilages fail to reach the mid line and articulate with each other in series. The twelfth and thirteenth ribs terminate in free costal cartilages. The rib series of *Dasyercus* differs very materially from the condition

Fig. 23.

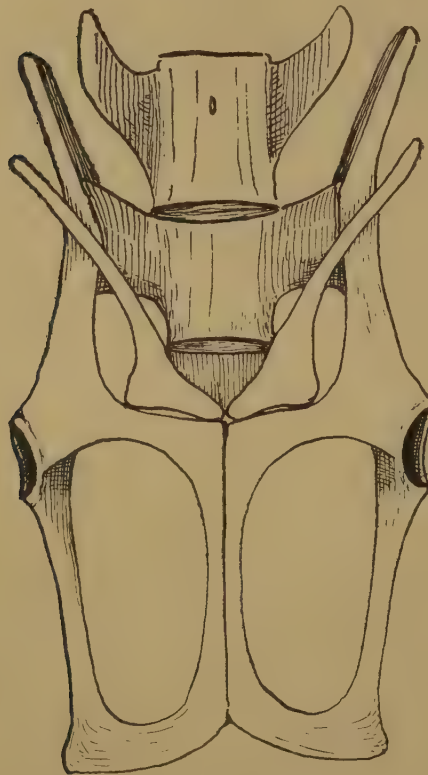
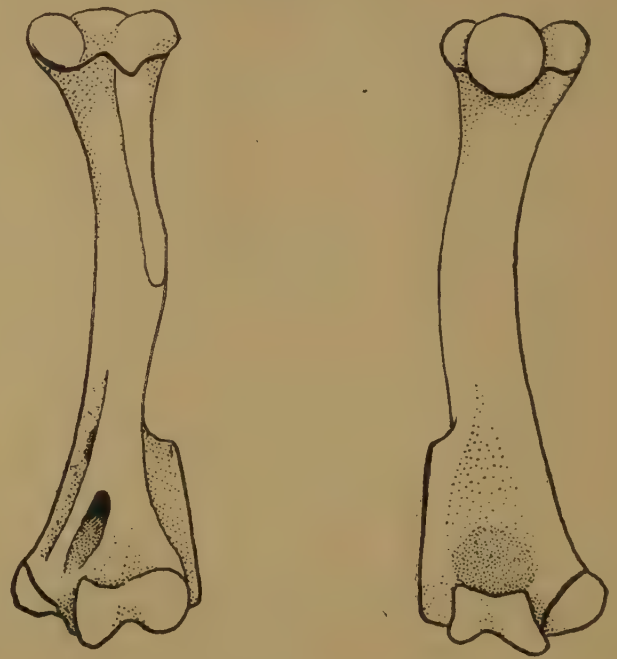
Pelvis of an adult female.  $\times 4$ .

Fig. 24.

Left humerus. Anterior and posterior aspects.  $\times 4$ .

described by Carlsson in *Dasyuroides*, for of the ribs in this allied form it is stated that "nine are fixed, and the remaining four are floating ribs". It would seem probable that Carlsson's description is erroneous.

The *Clavicle* (see fig. 21) is a slender bone, somewhat enlarged both at its sternal and acromial articular extremities. It is practically straight in its medio-lateral axis: convex in a ventral direction towards the mid line and concave laterally at its acromial end.

The *Scapula* (see fig. 22) is of the form usual in the other members of the Dasyuridae. The supraspinous fossa far exceeds the infraspinous fossa in extent. The spine and acromion are curved downwards as a scroll-like covering of the

infraspinous fossa and the axillary border of the bone is deflected in a dorsad direction, thus converting the infraspinous fossa into an incomplete osseous tube. The venter is flat over the greater part of its area, marked by a depressed line corresponding to the origin of the spine and convex over its axillary border. The acromion is well developed and articulates at its extremity with the clavicle. The coracoid is well developed, projecting over the top of the glenoid cavity, and connected with the clavicle by strong coraco-clavicular ligaments.

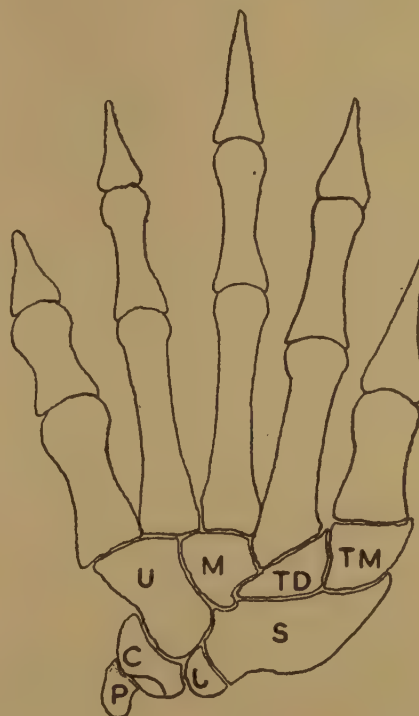
The *Pelvis* (see fig. 23) is of the usual marsupial form, with an ischiopubic symphysis of 10 mm. in a pelvis, the total antero-posterior length of which is 24 mm.

Fig. 25.



Left ulna and radius. Anterior and posterior aspects.  $\times 4$ .

Fig. 26.



Left manus. Dorsal aspect.  $\times 6$ . U=unciform. M=os magnum. TD=trapezoid. TM=trapezium. S=scaphoid. L=lunate. C=cuneiform. P=pisiform.

The ilia are elongated: their crests somewhat thickened and everted. The ischia are almost straight in their dorsal rami, the tuber ischii are thickened and slightly everted. The suprapubic bones measure 11 mm. in their longest axis and are of the typical form. The ilia articulate with one sacral vertebra only. The acetabula have wide ventral notches: the ligamentum teres is well developed.

The *Humerus* (see fig. 24) is a short bone with all muscular ridges highly developed. The lateral supracondylar crest is prominent, as it is in *Dasyurus* and in *Dasyuroides*. The deltoid ridge is well developed. The entepitrochlear foramen is large, as it is in *Dasyuroides*, and herein *Dasyercus* differs from some other members of the family in which this primitive feature is lacking. In the specimen figured,

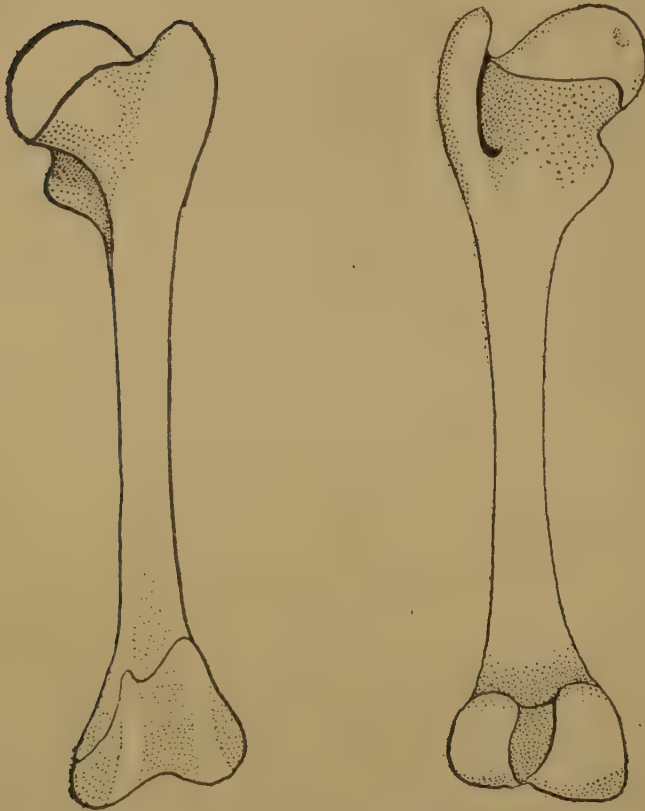


the epiphyseal lines for the upper extremity and for the medial condyle remain distinct.

The *Ulna* and *Radius* (see fig. 25) are slender bones, although muscular impressions are well marked upon them. The radius possesses a prominent flange upon its medial aspect. This flange reduces the interosseous interval in the lower third of the forearm, but the two bones remain distinct. The styloid processes of the two bones are practically on the same level.

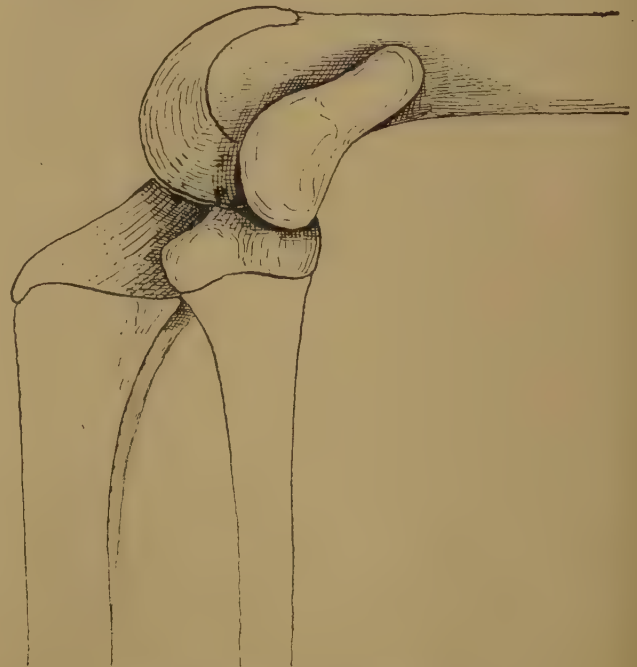
The *Carpus* (see fig. 26) shows a large scaphoid (radiale) and a small lunate (intermedium) articulating with the radius and a cuneiform (ulnare) articulating

[Fig. 27.



Left femur. Anterior and posterior aspects.  $\times 4$ .

Fig. 28.



Left knee-joint showing sesamoid.

with the ulna. The lunate is small but entirely separate from the scaphoid, articulating with it and with the cuneiform and unciform. The os centrale is not present as a separate element. A radial sesamoid is described in *Dasyuroides* by Carlsson, but it is not present in *Dasyercus*. The pisiform is well developed and somewhat rotated in a palmar direction. The third metacarpal is the longest and also the most slender bone of the series, the fifth digit is remarkably stoutly built in all its elements.

The *Femur* (see fig. 27) is a strongly built and well-marked bone. The great trochanter, like that of *Dasyurus*, is well developed, whereas according to Carlsson it is "a relatively small protuberance" in *Dasyuroides*. The upper and lower epiphyseal lines are distinct in the specimen figured. The large sesamoid,

to which the lateral head of the *M. gastrocnemius* is attached, articulates both with the lateral side of the lateral condyle of the femur and with the proximal extremity of the fibula (see fig. 28).

The *Patella* is represented only by a fibrocartilaginous induration in the quadriceps extensor tendon.

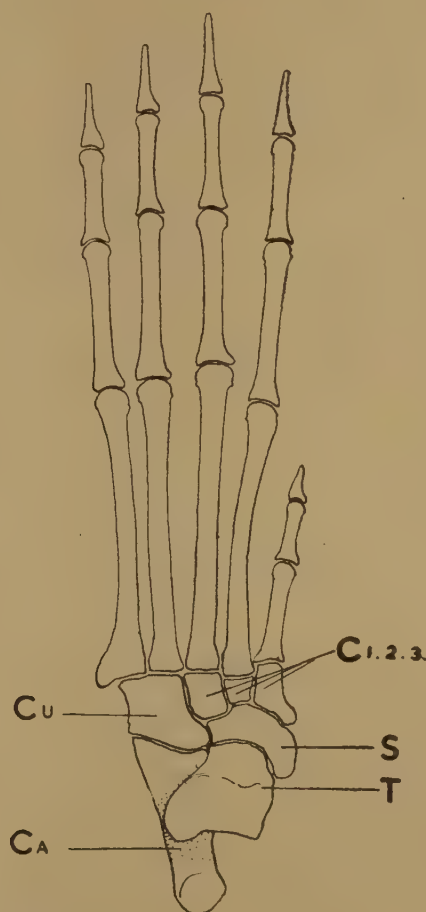
The *Tibia* (see fig. 29) has a well-marked crest and tuberosities.

Fig. 29.



Left tibia and fibula. Anterior aspect.  $\times 4$ .

Fig. 30.



Left pes. Dorsal aspect.  $\times 4$ . CU=cuboid. CA=os calcis  
S=scaphoid. T=talus. C=cuneiforms.

The *Fibula* is slender. The superior tibiofibular joint is confluent with the knee-joint. The two bones are separate in the whole of their length, being in contact only at their upper and lower extremities. The epiphyseal lines of both extremities are shown in the example figured.

The *Tarsus* (see fig. 30). The bones of the leg articulate only with the talus, which is a short compact bone. The talus and the cuboid touch each other over a very small area; but no definite articular facet is formed. The first cuneiform is well developed and supports the small first metatarsal. The third metatarsal is the longest.



## MYOLOGY.

*Muscles of the Head and Neck.*

The *Panniculus carnosus* in the region of the head and neck constitutes so uniform a subcutaneous muscular sheet that it is not profitable to attempt its subdivision into a series of named constituents such as may be recognized in mammals in which the differentiation of the sheet has proceeded to greater lengths. The massing of the fibres beneath the lips and eyelids constitute definite entities—the *orbicularis oris* and *orbicularis oculi* respectively (see fig. 98) : and well differentiated slips of muscle pass to the concha of the ear. For the rest, the whole of the anterior part of the body is clothed with a thin, but very distinct layer of platysma (see fig. 33).

Fig. 31.



The muscles of mastication of the right side. T=temporalis. M=masseter. B=buccinator.

*M. Buccinatorius* (see fig. 31) is continuous with the *orbicularis oris* and has its usual attachments.

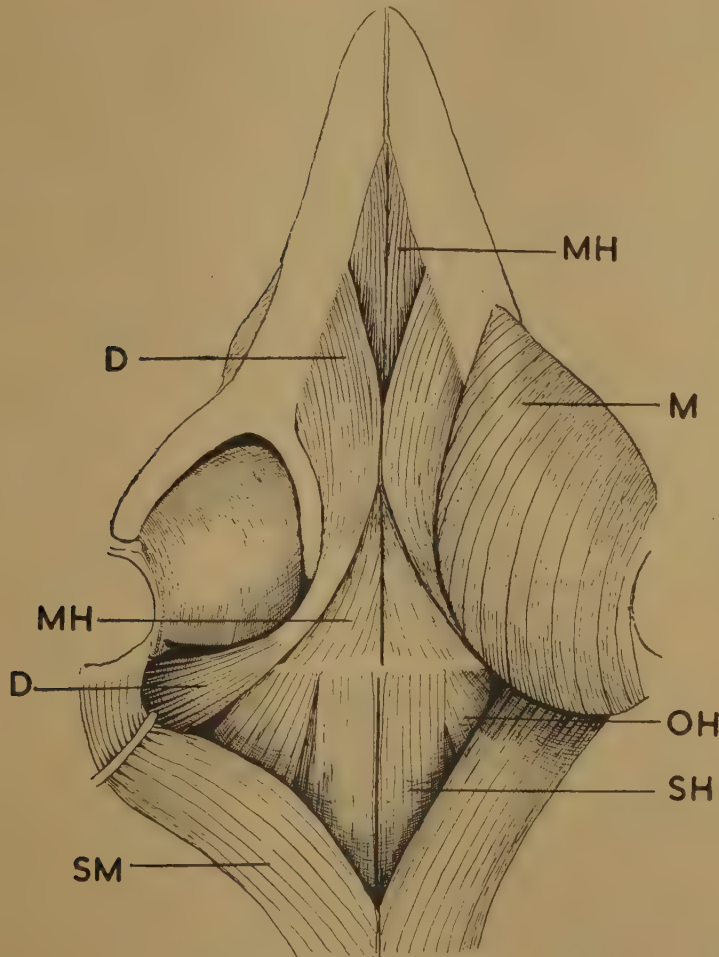
*M. Temporalis* (see fig. 31) is a well-developed and very powerful muscle. It is attached to the whole of the side of the cranium from the occipital crest to the postorbital fibrous septum and, passing deep to the zygoma, in two fairly well-defined layers, is inserted to the coronoid process of the mandible ; by tendon to the lateral and by fleshy fibres to the medial side. It is well defined and separated from all other muscles in its vicinity.

*M. Massetericus* (see fig. 31) is composed of two distinct layers. The superficial stratum is attached to the zygoma as far forwards as the globe of the eye and, passing backwards and ventrad and towards the medial line, wraps round the great convexity of the bulla, to be inserted to the median process of the backwardly prolonged mandible (see fig. 32). The deeper stratum is attached to the zygoma, deep to the foregoing portion, and passes to its attachment to the lateral aspect of the mandible over its ascending ramus. The whole muscular mass has a free anterior border that abuts upon the buccinator muscle of the cheek pouch. The superficial portion of the muscle sweeping over the bulla comes into relation with

the lateral portion of the anterior belly of the digastric. It overlaps the sternomastoid and comes into contact with the cervical extensions of the parotid and submandibular salivary glands.

*MM. Pterygoideus lateralis et medialis* are well developed and, at their attachment to the pterygoid plates, are represented by a fairly thick mass of fleshy fibres delaminated, as is usual, into a lateral and a medial stratum. As the common mass passes into the extremely narrow interspace between the bulla and the mandible it becomes compressed into narrow sheets of muscle that cover a wide

Fig. 32.



Muscles of the hyoid region. MH=mylohyoid. D=digastric. M=masseter. SM=sternomastoid. SH=sternohyoid. OH=omohyoid.

area of the medial aspect of the ramus of the mandible. The lateral pterygoid is not nearly so well developed as the deeper portion of the muscle. Its cranial attachment trespasses from the lateral surface of the lateral pterygoid plate to the surface of the alisphenoid in the temporal fossa anterior to the bulla. It passes as a thin band across the bulla and is attached to the ramus of the mandible. The medial muscle is attached to the plate and to the pterygoid fossa and passes downwards and backwards to the mesial aspect of the ramus of the mandible and to the inflected angle.



*M. Digastricus.* *Biventer maxillae* (see fig. 32) is composed of two large fleshy bellies with a strong intermediate tendon. The anterior belly is attached to the mandible over its medial margin, extending over about its posterior third to the medial process. The two anterior bellies meet in the mid line superficial to the mylohyoid. On the medial side of the bulla a strong intermediate tendon unites the anterior to the posterior belly. Unlike the condition described by Carlsson for *Dasyuroides* there is no attachment to the hyoid bone. The posterior belly is fan-shaped and is attached to the mastoid portion of the bulla deep to the sternomastoid.

*M. Mylohyoideus* (see fig. 32) is attached to the mandible as far forwards as the symphysis. The two muscles unite at a median raphe which passes backwards to the hyoid. At the hyoid attachment the fibres of the muscle receive an additional contribution on their superficial surface, so that here the muscle is composed of two distinct layers, of which the superficial layer has its fibres directed forwards to the mid line, while the deeper stratum has its fibres running slightly in the opposite direction.

*M. Geniohyoideus* is completely differentiated from the mylohyoid which covers it. The anterior attachment is to the symphysis menti deep to the anterior tendinous fibres of the mylohyoid, and the posterior attachment is to the body of the hyoid near the mid line.

*M. Hyoglossus* is represented by bilateral fusiform muscles attached deeply to the body of the hyoid and which, running forwards laterally, blend with the intrinsic muscles at the sides of the tongue by tendinous expansions.

*M. Sternohyoid* (see fig. 32) is normal in its attachments, but owing to the narrowness of the anterior part of the sternum it tapers abruptly to its sternal attachment. According to Young, the muscle passes to the mandible and has no attachment to the hyoid in *Phascolarctos*: but this would seem to be an unusual disposition in the marsupials.

*M. Sternothyroideus*, like the previous muscle, narrows at its sternal attachment and many of the fibres of both trespass onto the sternal extremities of the upper two or three ribs.

*M. Omohyoides* (see fig. 32) is well developed and is attached to the hyoid superficial to the attachment of the thyrohyoid. The intermediate tendon is ill-defined and a fibrous attachment to the clavicle, if present at all, is very trivial. Its distal attachment is to anterior border of the scapula near to the anterior (superior) angle.

*M. Sternomastoideus* (see fig. 32) is attached by a strong, rounded tendon to the ventral aspect of the pre- and mesosternum caudad to the sterno-clavicular articulation. Expanding to a rounded fleshy belly it gains attachment to the nuchal crest of the occipital bone passing forwards to the petro-mastoid portion of the temporal.

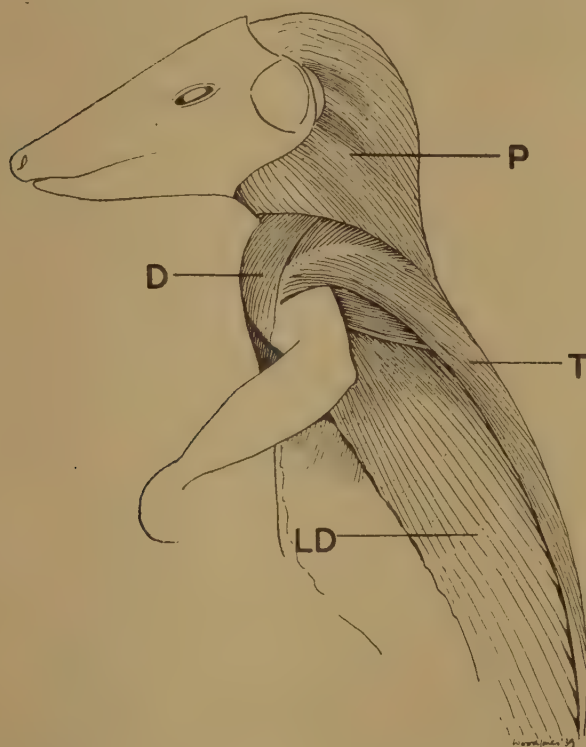
*M. Cleidomastoideus*, though separated by a considerable interval from the sternomastoid at the shoulder girdle, merges with the deeper fibres of that muscle at its cranial attachment.

*MM. Scaleni*, as in *Dasyurus* and other marsupials, are all situated dorsal to the brachial plexus and the subclavian artery.

*Muscles of the Fore-Limb.*

*M. Trapezius* (figs. 33, 34 and 36) is a large, flat, triangular sheet of muscle that is attached to the occipital crest of the skull, the spines of all the cervical and thoracic vertebrae and, by the intervention of fascial extensions, to spines caudal to the last rib-bearing vertebra. The lower fibres pass forwards to be attached to the spine of the scapula and have some fascial extensions to the infraspinatous fascia. The upper fibres pass, in common with the acromial portion of the deltoid, to the clavicle, the two muscles being inseparable from this point to the humeral attachment of the deltoid. This disposition, by which the cephalic fibres of the trapezius pass over the clavicle to a humeral insertion in common with the posterior

Fig. 33.



Superficial muscles of the left shoulder region. P=platysma. D=deltoid. T=trapezius.  
LD=latissimus dorsi.

fibres of the deltoid, constitutes the *M. Cephalohumeralis*. A similar condition is present in *Dasyurus*, according to MacCormick, but Carlsson does not note its occurrence in *Dasyuroides*.

*M. Deltoideus* (figs. 33-37) is a large and powerful muscle. It consists of three main portions attached respectively to the clavicle, the acromion and the spine of the scapula. The acromial portion becomes practically continuous with the cephalohumeralis fibres of the trapezius. The scapular portion is only doubtfully separated from the teres minor. The humeral attachment is made to the strongly developed deltoid ridge.

*M. Latissimus dorsi* (figs. 33-37) has the normal attachments to the lumbodorsal fascia and to the spines of the thoracic vertebrae with the variable exception of the

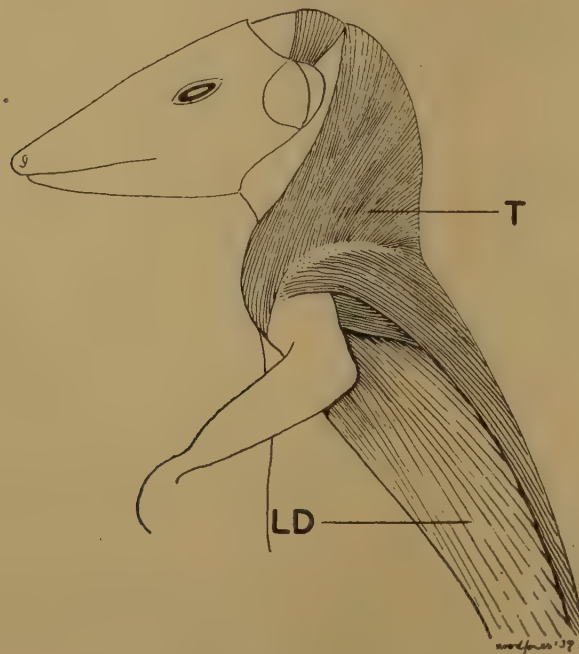


cephalic one or two. Towards its humeral attachment it becomes definitely divided into two portions, of which the most cephalic becomes partially blended with the caudal fibres of the teres major and the most caudal passes to the normal attachment to the bicipital groove of the humerus. There is no attachment to ribs or scapula. In its junction with the teres major it resembles the corresponding muscle in *Dasyurus*.

*M. Latissimocondyloideus seu dorsoepitrochlearis* (fig. 37) is a broad, thin band of muscle attached to the lower margin of the latissimus dorsi. Passing down the media aspect of the arm, it lies on the triceps and gains a flattened aponeurotic attachment to the olecranon process of the ulna independently of the triceps tendon. Its condition is as in *Dasyurus*.

*M. Rhomboideus* (fig. 35) is best described as a continuous sheet of muscle without any division into the two constituent elements usually described as MM. Rhomboideus major and minor. Most of its fibres run in the long axis of the body and

Fig. 34.



Muscles of the left shoulder region, after removal of the platysma. T=trapezius.  
LD=latissimus dorsi.

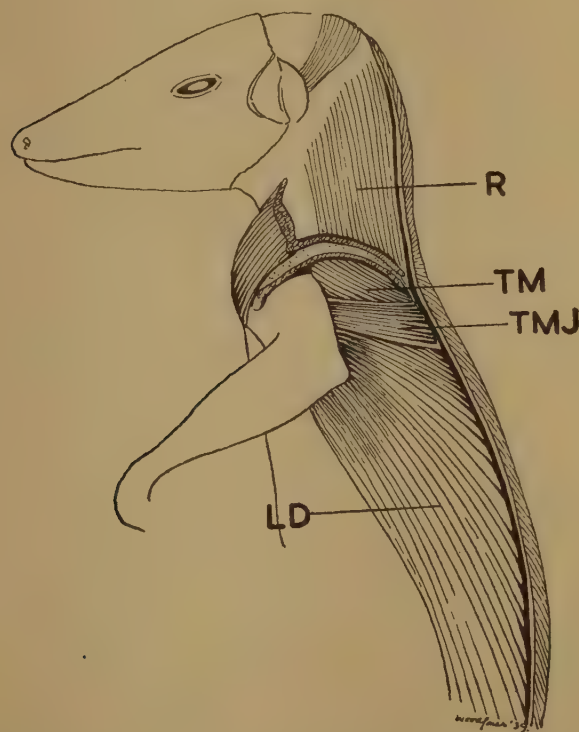
they pass, from a wide area of attachment to the occipital region of the skull and to the spines of all the cervical and the cephalic one or two thoracic vertebrae, to the whole length of the vertebral border of the scapula. This is the typical arrangement in the marsupials, *Dasyurus* being distinguished only by the limited attachment to the thoracic spines and the consequent more uniformly antero-posterior direction of its fibres.

*M. Ectopectoralis*. *Pectoralis major* consists of two parts. The most cephalic portion passes from the sternum and from fibrous tissue in front of the sternum common to the muscles of both sides. This part gains the normal attachment to

the humerus at the bicipital crest. The caudal and deeper part is represented by a narrow slip attached to the lower end of the sternum, the fascia common to it and the obliquus abdominis externus and to the linea alba. It joins the cephalic portion close to the attachment to the humerus. The caudal portion constitutes the *M. Pectoralis quartus* of some authors and as such its presence appears to be typical of the Dasyuroidae. The pectoralis quartus is intimately associated with fibres of the panniculus carnosus extending over the thoracic and abdominal areas.

*M. Entopectoralis.* *Pectoralis minor* lies deep to the other members of the pectoral group. It is attached to the sternum and to the sternal extremities of the five cephalic ribs, with the exception of the first of the series. It passes laterally

Fig. 35.



Muscles of the left shoulder region, after removal of the trapezius. R=rhomboideus. TM=teres minor. TMJ=teres major. LD=latissimus dorsi.

to the shoulder girdle and humerus, being attached to the coracoid process, the capsule of the shoulder joint and to the upper part of the humerus immediately distal to the capsule. By a fascial extension it also joins the tendon of the supraspinatus. In *Dasyurus* it is said by MacCormick to have no attachment to the coracoid.

*M. Subclavius* is a small muscle attached to the costal cartilage of the first rib, from which it passes to the clavicle and acromion.

*M. Serratus anterior seu magnus* forms a continuous sheet with *M. Levator scapulae*. The cephalic fibres of the muscle are attached to the transverse processes of the lowest four or five cervical vertebrae. The caudal part of the muscle is



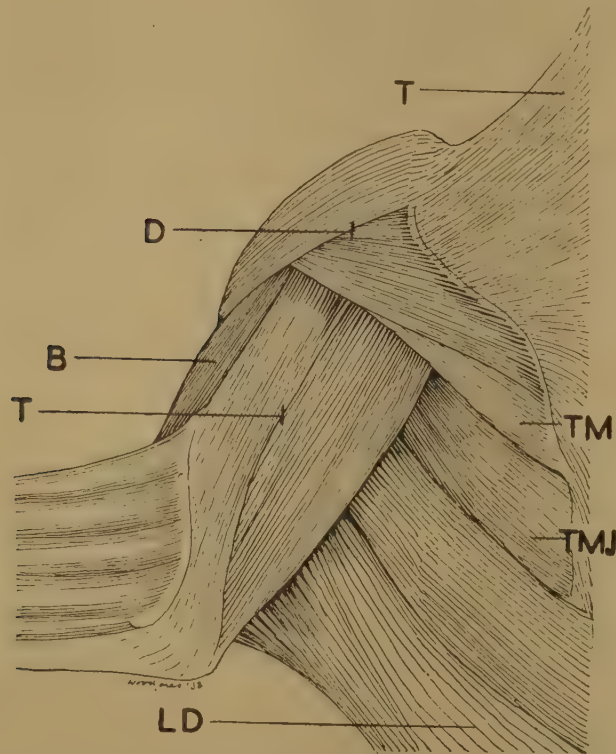
attached to the seven anterior ribs. The entire sheet is attached continuously to the whole length of the vertebral border of the scapula.

*M. Teres major* (fig. 35) is a well-developed muscle and has the normal attachments, but with an unusually large extension to the venter of the scapula, where it is in close apposition with the subscapularis.

*M. Teres minor* (fig. 35) is a poorly differentiated muscle attached to the axillary border of the scapula and only partially separable from the scapular extension of the deltoid.

*M. Supraspinatus* is a large fleshy muscle with normal attachments to the supraspinous fossa of the scapula. At its humeral attachment to the greater tuberosity it is intimately associated with the tendon of the entopectoralis.

Fig. 36.



Muscles of the dorsal aspect of the left shoulder and arm. T=trapezius. D=deltoid. B=biceps. T=triceps. LD=latissimus dorsi. TM=teres minor. TMJ=teres major.

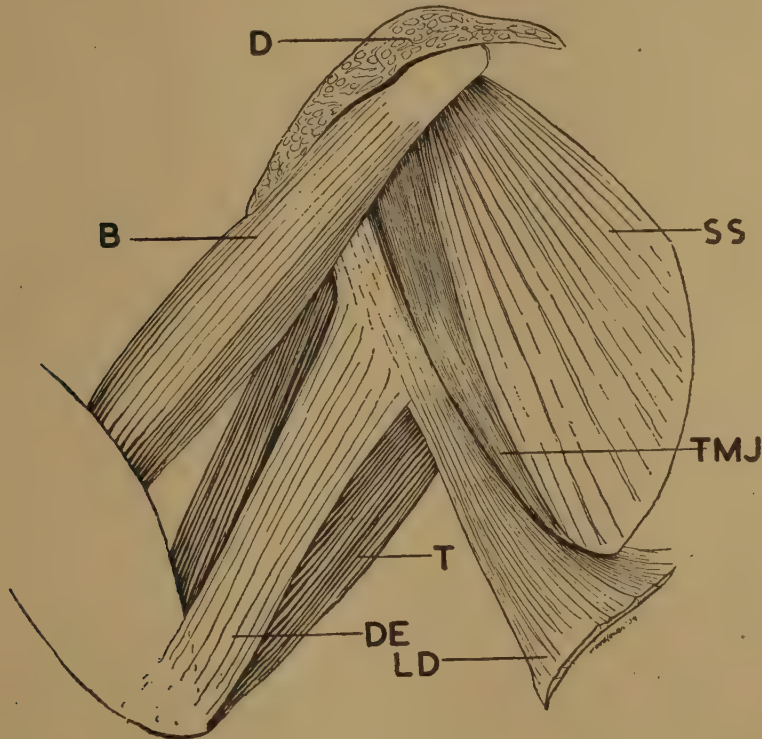
*M. Infraspinatus* is a very small muscle wholly covered by the scapular portion of the deltoid and that part of it which is separable as the teres minor. The humeral attachment is normal.

*M. Biceps brachii* (figs. 36 and 37) is double, both in its proximal and distal attachments. For the most part, but not entirely, the coracoid portion gains attachment to the tubercle of the radius and constitutes the coracoradialis, whereas the glenoid portion is attached to the coronoid process of the ulna, constituting a glenoulnaris. The exception to this diagrammatically simple separation of coracoradialis and glenoulnaris is that a small contribution from the glenoid tendon passes to the radial-sided part of the muscle. The whole muscle is strongly developed and resembles that in *Dasyurus* and some other marsupials.

*M. Coracobrachialis* is an extremely small muscle attached proximally to the coracoid process and distally to the humerus for only a short distance distal to the capsule of the shoulder joint. It represents only the most cephalic portion of the coracobrachialis complex—the coracobrachialis brevis vel superior of Wood—or the *M. rotator humeri*. The condition is similar in both *Dasyuroides* and *Dasyurus*.

*M. Brachialis*. *Brachialis anterior* is attached proximally to the lateral and posterior aspect of the humerus, deep to the lateral head of the triceps. The muscle winds round to the anterior surface of the humerus and becomes tendinous just above its attachment to the coronoid process of the ulna.

Fig. 37.



Muscles of the shoulder and arm. Ventral aspect of right limb. D=cut-edge of deltoid. B=biceps. SS=subscapularis. TMJ=teres major. LD=latissimus dorsi. DE=dorsoepitrochlearis. T=triceps.

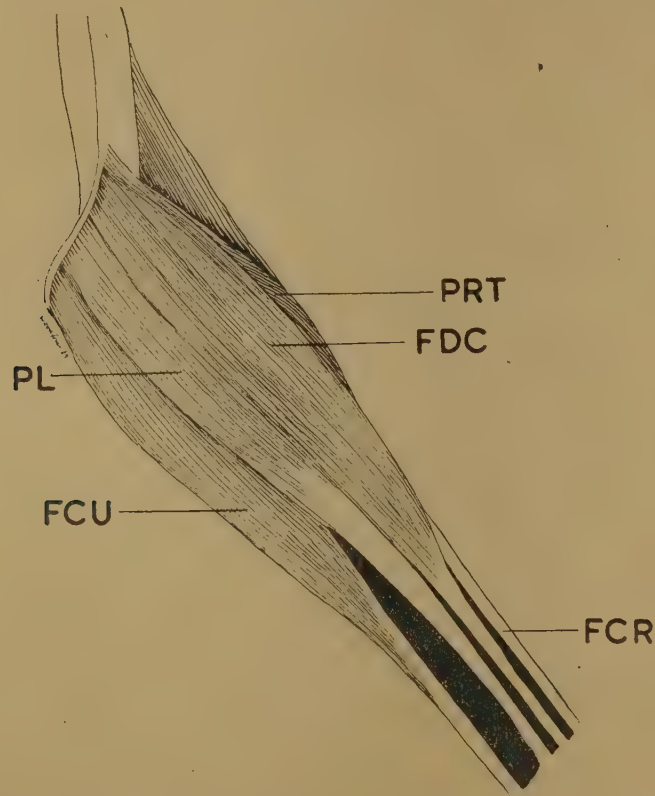
*M. Triceps* (figs. 36 and 37) is a large and complicated muscle, consisting of (a) a scapular head attached to the axillary border of the scapula; (b) a complex lateral head attached to the lateral aspect of the humerus; and (c) a complex medial head attached to the posterior and medial aspects of the humerus. The distal attachment of this very complex mass is made to the apex and lateral margin of the olecranon process of the ulna.

*M. Anconeus*. The so-called anconeus externus is inseparable from the medial head of the triceps, and the anconeus internus is only represented by an extremely small element. A few fibres passing from the posterior surface of the medial condyle of the humerus to the olecranon process constitute the sole justification for including it in the myology of *Dasyercus*.



*M. Brachioradialis.* *Supinator longus* (fig. 39) is a comparatively well-developed muscle separate at its humeral attachment from the radial extensor but lying closely approximated to it. It is attached high up on the lateral supracondylar ridge and its tendon passes over the distal extremity of the radius and gains attachment to the scaphoid and lunate carpal bones, the ligaments of the wrist joint and the base of the second digit. The muscle appears to be far better developed in *Dasycercus* than in *Dasyurus* and it resembles that in *Phascogale* : but in passing to the base of the second digit it appears to be extended more distally than in any of its near allies.

Fig. 38.



Muscles of the medial aspect of the left forearm. PRT=pronator radii teres. FDC=flexor digitorum communis. FCR=flexor carpi radialis. FCU=flexor carpi ulnaris. PL=palmaris longus.

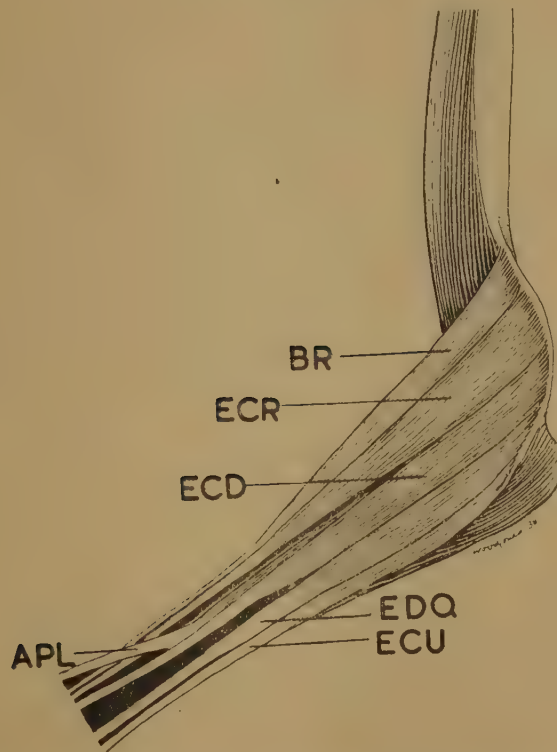
*M. Extensor carpi radialis* (fig. 39). In no examples did this simple muscle mass show any sign of subdivision. Its proximal attachment is to the lateral supracondylar ridge of the humerus immediately distal to the brachioradialis and distally it passes to the base of the third metacarpal with a small and variable extension to the second.

*M. Extensor digitorum communis* (figs. 39 and 40) is attached to the lateral condyle of the humerus by the common extensor tendon. Just proximal to the wrist joint it divides into four fine tendons that pass to digits 5, 4, 3 and 2. These tendons are crowded together in the interval between the distal ends of the radius

and ulna. The attachments to the dorsum of the digits are effected in the typical manner.

*M. Extensor carpi ulnaris* (fig. 39) is, at its attachment to the lateral condyle of the humerus, intimately blended with the extensor quinti digiti. This fusion of the two muscles is maintained in the proximal part of the forearm and it is only when the two tendons are developed, distal to the mid point of the forearm, that the individuality of the two elements is established. The tendon of the extensor carpi ulnaris lies on the ulnar side of that destined for the postaxial digits and, lying with it in the same groove, passes to the radial side of the base of the metacarpal bone of the fifth digit.

Fig. 39.



Muscles of the lateral aspect of the left forearm. BR=brachioradialis. ECR=extensor carpi radialis. ECD=extensor communis digitorum. APL=abductor pollicis longus. EDQ=extensor digiti quinti. ECU=extensor carpi ulnaris.

*M. Extensor proprius digiti quinti. Extensor secundus digitorum* (figs. 39 and 40) lies to the radial side of the common mass comprising the extensor carpi ulnaris and its tendon becomes distinct below the mid point of the forearm. Lying to the radial side of the tendon of the flexor carpi ulnaris it splits into two tendons that pass to the dorsal extensor expansions on the basal phalanges of digits 4 and 5.

*M. Extensor digitorum profundus* (fig. 40) is a compound muscle of which the separate named elements (extensor pollicis, indicis) cannot be separated to any advantage in the way of a gain of clarity in nomenclature. The fleshy part of the muscle is small and its proximal attachment is made mainly to the ulna as high as



the olecranon. A short distance above the wrist joint it gives rise to four tendons that pass deep to those of the extensor digitorum communis to the dorsal extensor expansions on digits 4, 3 and 2 and as the sole long extensor to digit 1. This preaxial tendon represents the *M. Extensor pollicis longus*. There is no trace of *M. Extensor pollicis brevis*.

*M. Abductor pollicis longus vel M. Extensor ossis metacarpi pollicis* (fig. 39) is a very well-developed muscle. Its proximal attachment is made to ulna, radius and interosseous membrane. The tendon, which emerges from the fleshy belly some distance above the wrist joint and passes superficial to the tendons of the extensor carpi radialis and brachioradialis, is attached to the base of the metacarpal of digit 1.

Fig. 40.



The arrangement of the extensor tendons of the digits of the manus. EDC=extensor digitorum communis. EDP=extensor digitorum profundus. EDQ=extensor proprius digiti quinti.

*M. Supinator.* *Supinator brevis* is rather a small muscle. It is attached in the normal manner to the lateral condyle of the humerus and passes distally to be attached to about the proximal fourth of the shaft of the radius.

*M. Pronator radii teres* (fig. 38) is a small muscle that, at its proximal end, is completely covered by the other muscles attached to the medial condyle of the humerus. It is attached somewhat deeply to the anterior aspect of the medial condyle and passes obliquely across the forearm to its attachment to the lateral aspect of the middle third of the radius. There is no ulnar component of the muscle.

*M. Flexor carpi radialis* (fig. 38) is only separable from the flexor digitorum complex at the point at which its tendon is developed in the lower half of the

forearm. Proximally it is attached to the medial condyle of the humerus but, like the pronator radii teres, it is deep to the superficial part of the flexor digitorum complex, with the fibres of which it is intimately blended. The fleshy belly gives rise to a slender tendon that emerges on the radial side of the flexor digitorum complex below the mid point of the forearm. It passes separately over the wrist joint and is attached to the bases of metacarpals 2 and 3, with extensions to the radial-sided carpal bones. In all respects it resembles the same muscle in *Dasyurus*.

*M. Palmaris longus* (fig. 38) is a well-developed muscle with a large fleshy component attached to the medial condyle of the humerus between the flexor digitorum complex and the flexor carpi ulnaris. The tendon is flat, superficial and conspicuous; it terminates distally in the normal way by joining the palmar fascia and becoming divided into four main digital extensions.

*M. Flexor digitorum communis* (fig. 38). The flexor digitorum complex is incapable of division into its usual named components. As in *Dasyurus*, four main elements may be recognized:

(a) A bulky mass, attached proximally to the medial condyle and medial supracondylar ridge of the humerus that, after becoming inextricably blended with the other portions, gives rise to four delicate tendons that pass to be attached to digits 5, 4, 3 and 2 in the manner typical of *M. Flexor digitorum perforatus*.

(b) A part, deep to the flexor carpi ulnaris, attached to the medial humeral condyle and the anterior surface of the ulna.

(c) A part attached proximally to the anterior surface of both ulna and radius.

(d) A smaller, but separate portion attached deeply to the medial condyle of the humerus.

Parts (b), (c) and (d) give rise to a large common tendon that divides, deep to the flexor retinaculum, into five tendons that are attached to their respective digits in the manner typical of *M. Flexor digitorum perforans*.

In all specimens the preaxial digit appeared to possess only one long flexor tendon.

*M. Flexor carpi ulnaris* (fig. 38) is a large muscle, well differentiated from the rest of the mass at the medial condyle of the humerus. The tendon appears below the mid point of the forearm and muscle fibres join it on its deep and postaxial aspects as far distal as the wrist joint. Distally it is attached to the pisiform bone in the normal manner, its tendon having the usual carpal extensions.

*M. Pronator quadratus* is a well-developed muscle covering the anterior surface of radius and ulna in the distal half of the forearm.

*MM. Lumbricales*, four in number, are well developed and have the normal attachments.

*MM. Interossei palmares* comprise the typical adductors of digits 1, 2, 4 and 5, arranged in the normal manner.

*MM. Interossei dorsales* are normal, the third digit receiving the attachments of two muscles, the second and fourth only one.

The *abductor digiti quinti* and *abductor pollicis* complete the series of digital abductors. In addition there is a complete series of *flexors breves*.

In *Dasyurus*, MacCormick reported the *M. Palmaris brevis* to be "well represented": but in *Dasyercus* its identification, probably on account of the small size of the manus, was not determined beyond all doubt.

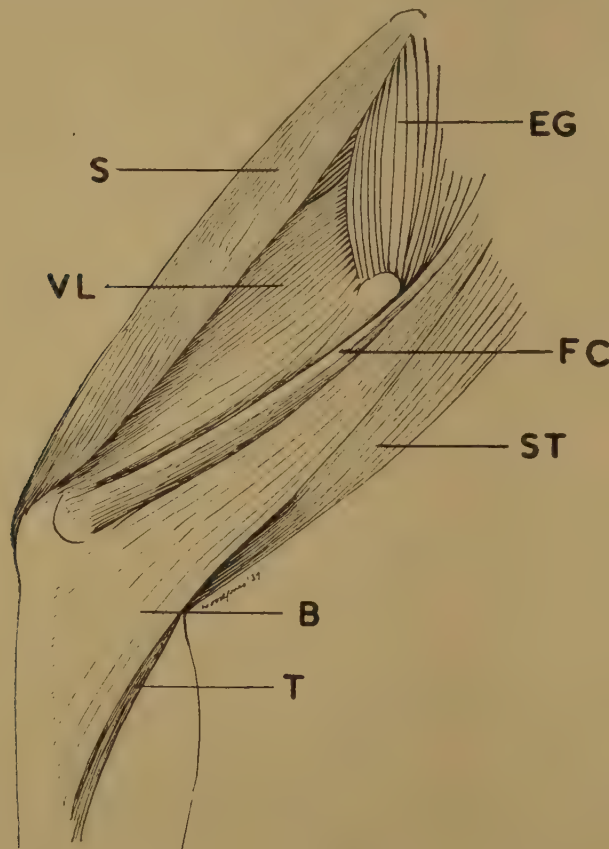


*Muscles of The Hind Limb.*

The gluteal muscles do not constitute a very bulky or conspicuous group. Their differentiation is not so complete as it is in many Eutherian mammals and only three elements are separable as distinct entities.

*M. Ectogluteus.* *Gluteus maximus* (fig. 41) is the most superficial member of the group. It is a thin flat sheet of muscle somewhat triangular in shape, with its base at the vertebral column and dorsum ilii and its apex at the great trochanter. Its cephalic attachment is made to the dorsum ilii and to the spines of the sacral

Fig. 41.



Superficial muscles of the dorsal surface of the left thigh. S=sartorius. VL=vastus lateralis. EG=ectogluteus. FC=femorococcygeus. ST=semitendinosus. B=biceps. T=triceps.

vertebrae by a thin fascial extension from its main attachment. To the great trochanter its attachment is made by a discrete tendon, there being no extension to the fascia of the thigh. The fibres of the muscle run almost directly in the long axis of the body and, unlike the muscle in *Dasyurus*, it completely covers the mesogluteus. In *Notoryctes* Thompson described an extension of the trochanteric tendon to the fascia of the thigh; but in *Dasyurus*, as in *Dasyurus*, no such extension is present. There is therefore no representative of the *M. tensor fasciae latae* (*M. tensor fasciae femoris*) and it would almost seem that Carlsson is in error in describing this muscle as a distinct entity in *Dasyuroides*.

*M. Femorococcygeus.* *Agitator caudae* (fig. 41) is a well-developed muscle which at its cephalic attachment is closely associated with the ectogluteus. It is attached by a thin fascial lamella to the spines of the sacral and proximal caudal vertebrae and to the tuber ischii. Its most anterior fibres lie superficially to the posterior border of the ectogluteus. It is distinctly divided into two laminae. The superficial portion is long and strap-like and passes to be attached to the femur almost down to the lateral condyle, some of its fibres passing by a fascial extension to the lateral side of the knee-joint. The deeper part of the muscle is attached just below the great trochanter. The low attachment of the superficial portion to the femur agrees well with Cunningham's description of the muscle in *Thylacinus* and Thompson's in *Notoryctes*: but it differs from the higher attachment described by Carlsson in *Dasyuroides* and by MacCormick in *Dasyurus*. Only the anterior margin of the muscle remains uncovered by the biceps femoris and as a rule the cephalic extremity of the muscle is completely covered by the biceps.

*M. Mesogluteus.* *Gluteus medius* (fig. 42) is a small muscle that is entirely covered by the ectogluteus. It lies in almost the same axis as the superficial muscle and is a muscle of basal simplicity. It is attached to the dorsum ilii and its fibres converge towards the great trochanter. No separable layers can be recognized as, according to MacCormick, they may be in the muscle of *Dasyurus*. The attachment to the great trochanter is anterior to and separate from that of the ectogluteus.

The last member of the group is probably representative of the combined *gluteus minimus* and *piriformis*, for it arises both within and without the pelvis in the region of the sacrosciatic foramen and passes over the emerging sciatic nerve to be attached to the great trochanter of the femur. Its fibres are focused on the great trochanter and the majority of them run at right angles to those of the other gluteal muscles.

No representative of a fourth gluteal muscle—the *gluteus quartus* or *scansorius*—is present. The muscles of the gluteal group show no very noteworthy departure from the condition present in the majority of the Dasyuridae. The most outstanding individuality seems to be the conjoined condition of *gluteus minimus* and *piriformis*. But this state of affairs, according to Thompson, is constant in *Notoryctes* and is present in some other marsupials, as well as in many of the Insectivora. From *Dasyuroides*, *Dasyercus* appears to differ only in the relatively smaller size and unilaminar condition of the mesogluteus.

*M. Caudofemoralis.* *Ischiofemoralis* (fig. 42) is a well-developed muscle attached mainly to the sacrotuberous ligament but with additional bony origin from the sacral vertebrae. The main axis of its fibres is obliquely downwards and laterally to the femur to the middle third of the postero-lateral aspect of which it is attached. In *Dasyurus* the vertebral and sacrotuberous attachments are described by MacCormick as being separated by a considerable interval and in many marsupials the attachment to the femur is more extensive than it is in *Dasyercus*.

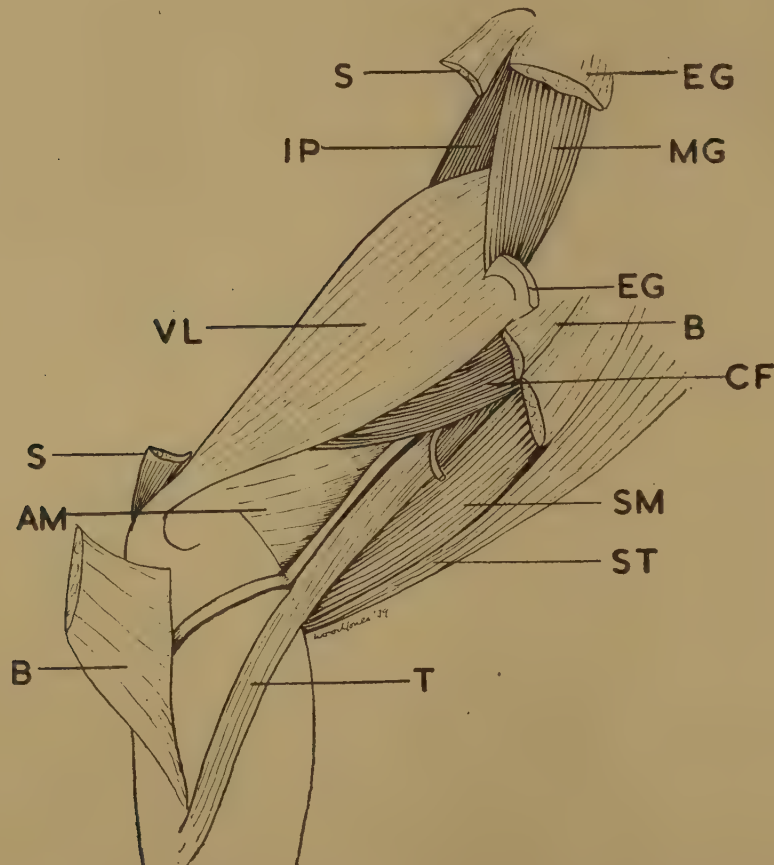
*M. Quadratus femoris* (fig. 43) is also a well-developed and well-differentiated muscle and the coexistence of a large quadratus femoris with equally well-developed caudofemoralis and adductor magnus is a point of some importance.



The condition is paralleled in *Dasyurus*. It is attached medially to the tuber ischii deep to the emerging sciatic nerve and passing almost horizontally laterally is attached to the posterior aspect of the great trochanter and to the shaft of the femur over about the upper sixth of its length.

*M. Obturator internus* and *gemelli*. The muscle mass representing these three elements is not well differentiated into its constituent parts. The intrapelvic element is relatively small. In *Sarcophilus*, Macalister reported the obturator

Fig. 42.



Deeper muscles of the dorsal surface of the left thigh. S=sartorius. EG=ectogluteus. MG=mesogluteus. IP=iliopsoas. VL=vastus lateralis. B=biceps. CF=caudofemoralis. SM=semi-membranosus. ST=semitendinosus. AM=adductor magnus. T=tenuissimus.

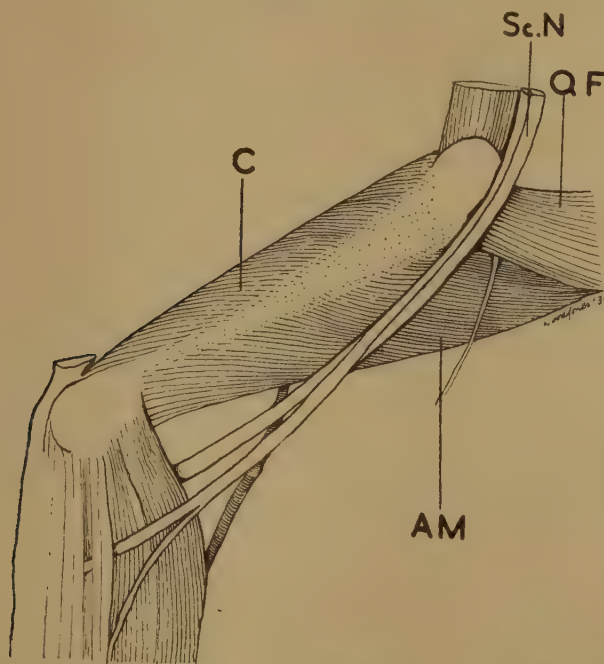
to be absent, the whole of the muscle being extrapelvic in origin and therefore constituted by the gemelli. In *Dasyurus*, however, the intrapelvic portion is well developed and the gemelli are represented by a single muscle. *Dasyercus* would therefore appear to show a very generalized condition of this muscle complex.

*M. Obturator externus* is a well-developed muscle normal in its attachments and corresponding to the condition described in other polyprotodont marsupials. The attachment to the great trochanter, which is in close proximity to that of the obturator internus, exceeds the limits of the digital fossa.

*M. Biceps femoris* (figs. 41 and 42) is a large and powerful muscle and in the undisturbed condition conceals most of the muscles of the back of the thigh. Its upper attachment is partly fascial and partly, directly from the tuber ischii, by tendon. It lies superficial to the femorococcygeus and passes downwards towards the knee-joint to be attached by a wide fascial lamella to nearly the proximal half of the lateral aspect of the tibia from its lateral condyle downwards. From this fascial expansion an extension runs proximally to the lateral margin of the quadriceps tendon. There is no attachment directly to the fibula.

*M. Tenuissimus. Bicipiti accessorius* (fig. 42) is well developed, as is usual in the Dasyuridae. Concerning this muscle there is some confusion in the literature, since it is sometimes regarded as merely a part of the biceps femoris and is

Fig. 43.



Deepest layer of muscles of the dorsal surface of the left thigh. C=crureus. QF=quadratus femoris. AM=adductor magnus. Sc.N=sciatic nerve.

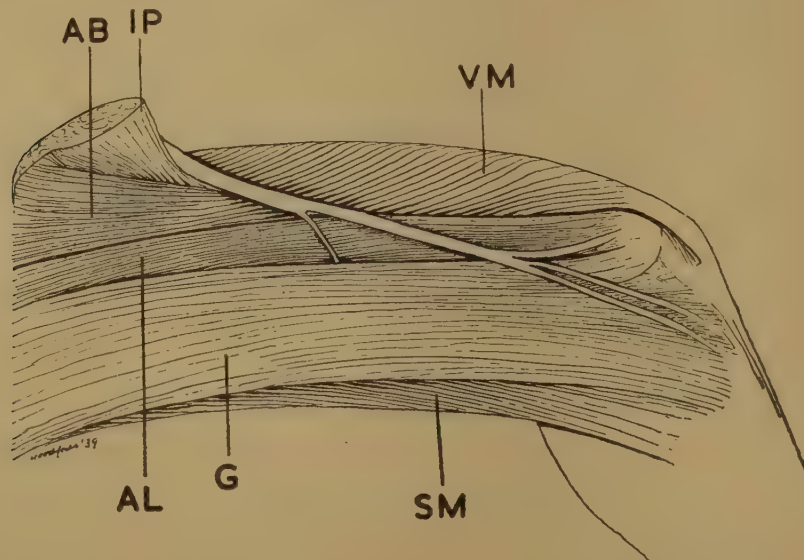
described as the deep caudal portion of that muscle. In *Dasycercus* there is no possibility of confusing the two muscles, for the tenuissimus is deep to and separated from the biceps in the whole of its extent. Its cephalic attachment is deep to the fascial attachment of the biceps. It is an elongated, thin strand of muscle which passes down the back of the thigh deep to the biceps and to the caudofemoralis. In this it resembles the muscle in *Dasyurus* and it is possibly in error that Thompson describes it as lying superficial to the caudofemoralis in *Notoryctes*. It lies immediately behind the great sciatic nerve and in front of the semimembranosus. It passes over the lateral head of the gastrocnemius and gains a fascial attachment to the lateral aspect of the leg over a small area immediately distal to the biceps. Part of this fascial attachment is made direct to the fibula.



*M. Semitendinosus* (figs. 41 and 42) has no attachment to the caudal vertebrae. It lies immediately deep to the biceps femoris where its tendon joins the lateral aspect of the tuber ischii. It passes down the back of the thigh to gain attachment to the medial aspect of the tibial tuberosity, with practically no downward extension to the crest or shaft of the tibia. The muscle is simple in its whole extent and has no tendino-fibrous intersection as in *Dasyurus* or subdivision as in *Notoryctes*.

*M. Semimembranosus* (figs. 42, 44 and 45) is a large and well-differentiated muscle passing down the back of the thigh from the tuber ischii to the medial tuberosity of the tibia. On the back of the thigh it is concealed by the semitendinosus and on the ventral aspect it lies under cover of the gracilis. Its fibres run parallel from the ischium to the tendon of attachment to the tibia. This attachment is effected deep to the tendon of the gracilis but the distal extension of the attachment extends further down the tibia than the gracilis.

Fig. 44.



Superficial muscles of the ventral surface of the left thigh. AB=adductor brevis. IP=iliopsoas. VM=vastus medialis. AL=adductor longus. G=gracilis. SM=semimembranosus.

*M. Sartorius. Ilio-tibialis* (figs. 41 and 42) is a very well-developed muscle constituting the most conspicuous muscle mass on the preaxial margin of the limb. Its cephalic attachment is made by tendon to the anterior spine of the ilium and to a small area of the ligamentum inguinale. The fleshy muscle passes down the front of the thigh and, becoming tendinous, passes over the patellar fibrocartilage and is attached by a wide fascial extension to the medial aspect of the upper end of the tibia, also gaining some attachment to the tendon of the quadriceps. At its cephalic extremity it overlaps the anterior margin of the ectogluteus.

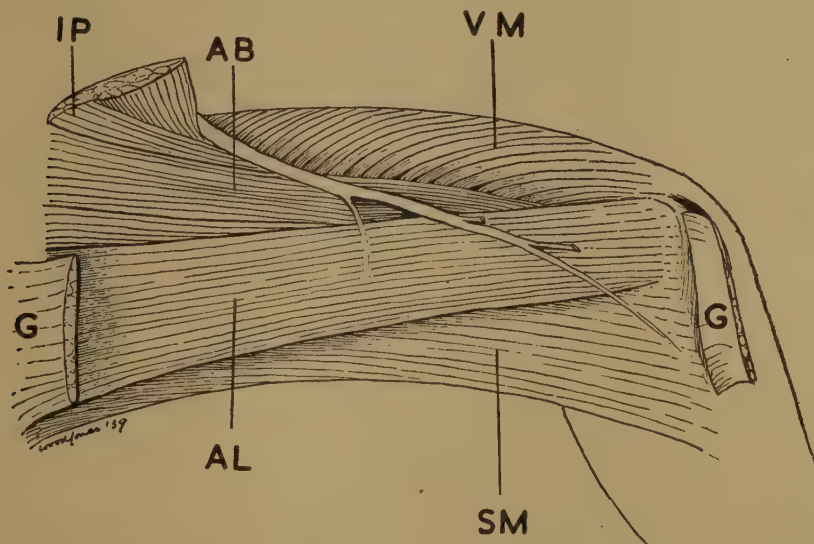
*M. Rectus femoris.* In one specimen this muscle possessed a single isolated attachment to the anterior surface of the ilium at the site of the anterior inferior iliac spine. In others an imperfectly differentiated extension gained attachment to the dorsum ilii immediately above the acetabulum. In no case could the muscle

be described as being attached by two separate heads, and in *Dasyurus*, in which MacCormick described the muscle as bicipital, he admits that "a pin can with difficulty be inserted between them". The muscle is narrow and flattened, being compressed between the crureus and the vastus lateralis. It is, however, a well-differentiated entity until it joins the quadriceps extensor tendon.

*M. Vastus lateralis* (figs. 41 and 42) is by far the largest and most conspicuous of the quadriceps extensor group of muscles. Its anterior margin overlaps the rectus femoralis. Its attachments to femur, patellar fibrocartilage and tibia are normal. Its large size in comparison with that of the vastus medialis is typical of all the near allies of *Dasyercus*.

*Mm. Vastus medialis* and *intermedius*. *Profundus* or *Crureus* (figs. 43, 44 and 45) are blended at their proximal attachment but their separation is apparent on the surface of the common mass, even in the upper part of the thigh, and the two muscles become entirely separate at their attachment to the quadriceps tendon.

Fig. 45.



Deeper muscles of ventral surface of the left thigh. IP=iliopsoas. AB=adductor brevis. VM=vastus medialis. G=cut-ends of gracilis. AL=adductor longus. SM=semimembranosus.

*M. Subcrureus*. Although in *Dasyurus* MacCormick describes this muscle as "well-developed", no muscle fibres recognizable as such were present in any specimen of *Dasyercus*.

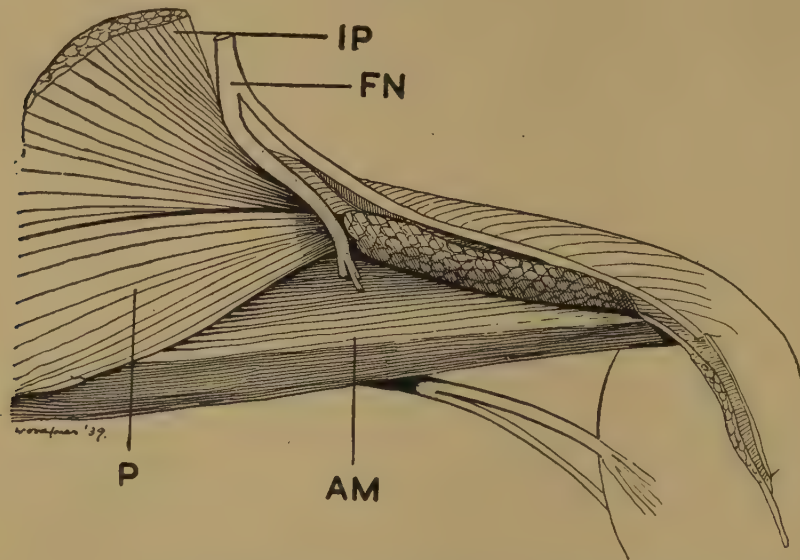
*M. Iliopsoas* (figs. 42, 44, 45 and 46). The psoas magnus, psoas parvus and iliacus are all normal in relative development and disposition when regard is had to the accounts published of the muscle complex in other polyprotodont marsupials. Psoas parvus and magnus are about equal in bulk. In *Dasyurus*, parvus exceeds magnus and in *Notoryctes* the reverse is the case. The iliacus is attached to the whole of the inner surface of the ilium and passes with the tendon of the psoas magnus to the trochanter of the femur.

*M. Gracilis*. *Adductor cruris* (figs. 44 and 45) is a well-developed muscle and is in the form of a wide quadrilateral sheet which covers the medial aspect of the



thigh. It almost entirely covers the remaining members of the adductor femoris complex and lies over the upper (lateral) margin of the semimembranosus. It is attached above to the symphysis pubis and to the bone adjacent to it, with only a very indefinite extension to the marsupial bone. After crossing the medial aspect of the knee-joint it is attached by fascia to the medial border of the upper extremity of the tibia. From the upper border of this fascial attachment a definite slip passed, in two specimens, to the medial condyle of the femur. Save for the occasional femoral attachment, the condition of the muscle agrees with the general disposition in other polyprotodont marsupials.

Fig. 46.



Deepest muscles of the ventral surface of the left thigh. IP=iliopsoas. FN=nervus femoralis. AM=adductor magnus. P=pectineus.

*M. Pectineus* (fig. 46) is relatively well developed. Above, it is attached to the pubis and to the adjacent area of the marsupial bone. It passes obliquely across the thigh to be attached to the lower part of the lesser trochanter and upper third of the shaft of the femur. Unlike the muscle in *Dasyurus* and *Notoryctes* and other marsupials, it is a simple mass, showing no division into distinct superficial and deep parts.

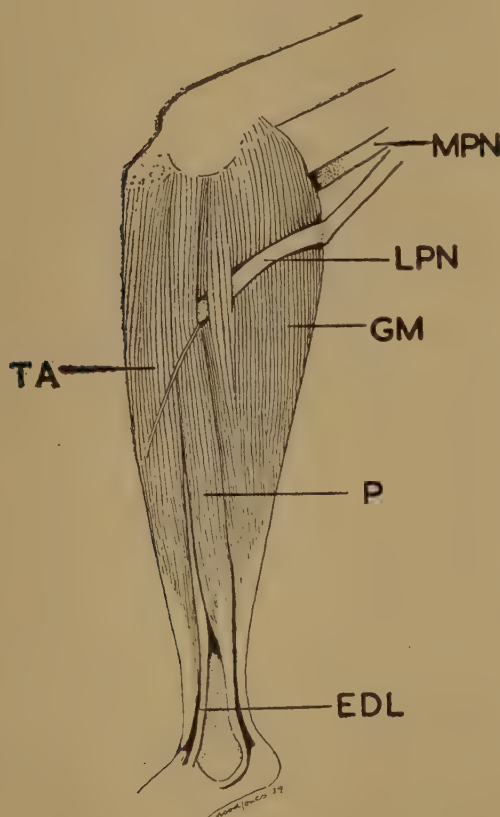
*M. Adductor longus* (figs. 44 and 45) is a strap-like muscle with parallel fibres running from the pubis to the medial aspect of the knee-joint. Above, it is attached to the pubis and by a minor extension to the marsupial bone. Below, it joins the lower end of the medial side of the femur with a definite extension to the medial tuberosity of the tibia.

I have no doubt that the muscle figured and described here is in fact the adductor longus, but evidently it is not identical with that described in *Dasyurus* under that name by MacCormick. MacCormick's muscle named adductor longus gained attachment to the femur behind and "higher up" than the attachment of pectineus

and it would almost seem that he had transposed the names adductor longus and brevis. By Carlsson, the adductor longus is indicated in her figure of *Dasyuroides* as the presemimembranosus. On the other hand, the muscle here described as adductor longus agrees with that in *Notoryctes* as described by Thompson.

*M. Adductor brevis* (figs. 44 and 45) is a well-differentiated muscle attached above to a wide area of the ischiopubic ramus and passing downwards and laterally to gain attachment to the mid point of the shaft of the femur.

Fig. 47.



Muscles of the lateral aspect of the left leg. MPN=medial popliteal nerve. LPN=lateral popliteal nerve. TA=tibialis anterior. P=peroneus. GM=medial belly of gastrocnemius. EDL=extensor digitorum longus.

*M. Adductor magnus* (figs. 43 and 46) is attached above to the ischial portion of the ischiopubic ramus and below to the distal third of the femur. In total mass it is somewhat smaller than the adductor brevis.

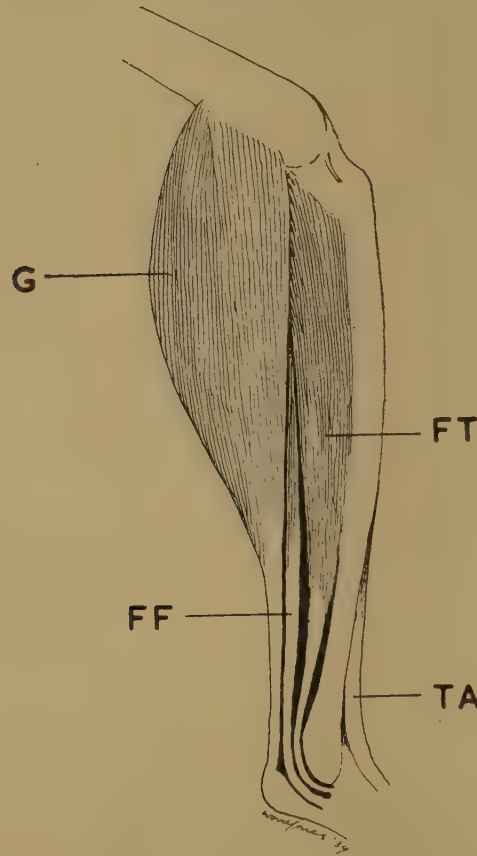
*M. Tibialis anterior* (figs. 47 and 48) is a strongly-developed muscle attached to the lateral tuberosity and to the lateral surface of the shaft of the tibia in its upper half. It also gains a slight attachment to the upper part of the interosseous membrane. This attachment, however, does not extend to the fibula. The tendon arises in the lower third of the leg and, passing to the dorsum of the foot, is attached to the first cuneiform bone, but more conspicuously to the base of the first metatarsal. In *Dasyurus*, according to MacCormick, no attachment is made



to the first metatarsal, but Thompson describes the metatarsal extension in *Notoryctes*.

*M. Extensor hallucis longus seu proprius* is apparently incorporated in the tibialis anterior, from which it is not possible to separate it, although a tiny thread-like tendon passing further distally on the minute hallux may perhaps represent it.

Fig. 48.



Muscles of the medial aspect of the left leg. G=lateral belly of gastrocnemius. FT=flexor tibialis. FF=flexor fibularis. TA=tibialis anterior.

*M. Extensor digitorum longus* (fig. 47) is attached to the lateral ligament of the knee-joint and to the head and upper two-thirds of the shaft of the fibula. The proximal attachment also extends to the interosseous membrane. The slender tendons pass across the dorsum of the foot to be attached in the normal manner to the four postaxial digits.

*M. Extensor digitorum brevis* is a very poorly-developed muscle. The small fleshy belly has its proximal attachment to a small area on the lower end of the fibula just above the ankle-joint. This little muscle mass gives rise to three tendons that have the usual attachments to the second, third and fourth digits. Its condition appears to be similar to that in other members of the *Dasyuridae*.

*M. Peroneus communis* (fig. 47). The peroneal group of muscles is strangely reduced or, perhaps, is but little differentiated. A common fleshy mass has attach-

ment to the lateral ligament of the knee-joint and to the head and upper part of the shaft of the fibula. This fleshy belly gives rise to a single tendon that passes behind the lateral malleolus. No tendon passes anterior to the malleolus. The single retro-malleolar tendon runs undivided to the postaxial border of the foot and, becoming flattened, is attached to the base of the fifth metatarsal, with a slip to the extensor of that digit and another to the dorsal aspect of the cuboid, from which slips pass to the extensors of the third and fourth digits. No extension of the tendon could be detected passing beneath the sole of the foot. This condition was identical in all specimens examined. It differs markedly from the description of the peroneal group of muscles by Carlsson in *Dasyuroides*, MacCormick in *Dasyurus* or Thompson in *Notoryctes*. In all other marsupials at least two peronei—longus and brevis—seem to be differentiated.

*M. Gastrocnemius* (figs. 47, 48 and 49) is in its typical form, the two bellies remaining separate in the proximal portion of the leg. The lateral head is attached mainly to the large sesamoid lying against the lateral condyle of the femur. It also gains attachment to the head and to a small area of the upper portion of the shaft of the fibula. A slip attached to the lateral condyle of the femur is separated from the main mass of the lateral head by the passage of the lateral popliteal nerve. The medial head is attached to the popliteal surface of the femur and to the medial condyle itself. The tendo Achillis shows the typical twist caused by the part of tendon derived from the medial head passing laterally, superficial to that derived from the lateral head.

*M. Soleus* is only doubtfully separable from the lateral head of the gastrocnemius.

*M. Plantaris* (fig. 49) is a large muscle, its bulk being much the same as that of the lateral head of the gastrocnemius with which, at its proximal end, it is associated. Its attachment is made in common with that of the lateral gastrocnemius, but it readily distinguished from that muscle by its occupation of a deeper plane in the calf and by the passage of the posterior tibial nerve. Its fleshy belly descends further distally than do either of the gastrocnemii and its tendon passes to the medial side deep to that derived from the medial gastrocnemius. On reaching the heel it gives a small slip to the medial side of the os calcis and then passes into the sole of the foot by continuing as the plantar fascia and the flexor digitorum brevis attached to it.

*M. Flexor digitorum tibialis* (fig. 48) is attached to the lateral ligament of the knee-joint and to the upper third of the posterior surface of the tibia. The tendon is developed in the lower third of the leg and, passing round the medial malleolus into the sole of the foot, it is attached to the base of the metatarsal bone of the preaxial digit. A slip from this tendon also joins the plantar fascia.

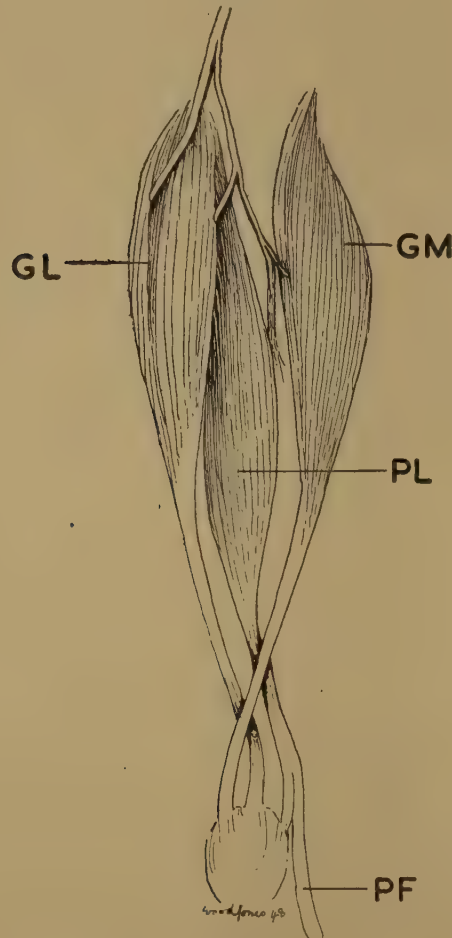
*M. Flexor digitorum fibularis* (fig. 48) is a well-developed muscle attached to the whole of the posterior surface of the fibula from head to malleolus. The broad tendon is developed in the lower third of the leg and it passes into the sole of the foot posterior and lateral to, and independent of, the tendon of the flexor tibialis and divides into perforating tendons for the four postaxial digits.

*M. Tibialis posterior* (fig. 50) is a tiny muscle attached proximally to the upper



extremity of the fibula with a slight extension to the interosseous membrane. The small fusiform fleshy belly soon gives rise to a long slender tendon which, on reaching the sole of the foot, passes over the scaphoid to the first cuneiform and to the base of the metatarsal of the first digit. In most marsupials the tibialis posterior is a small muscle and in many the attachment is made direct to the scaphoid as well as to the first cuneiform and metatarsal.

Fig. 49.

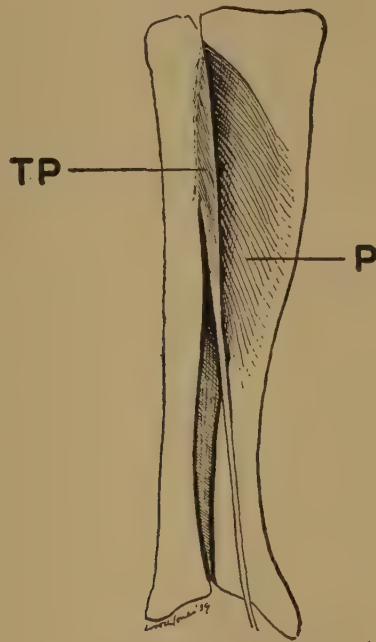


The composition of the gastrocnemius and plantaris. GM=medial. GL=lateral head of gastrocnemius. PL=plantaris. PF=extension of plantaris tendon to plantar fascia.

*M. Popliteus. Pronator tibiae. Peroneotibialis* (fig. 50) is well developed and occupies the whole of the proximal portion of the interosseous space. It is attached to the medial aspect of the head and about the upper third of the posterior surface of the fibula and passes obliquely distally towards the tibia, to the posterior surface of which it is attached down to just below its mid point. The small tibialis posterior is separated from the muscle by the intervention of a strong layer of aponeurotic fascia.

*M. Flexor digitorum brevis.* *M. Flexor digitorum perforatus* is a thin sheet of muscle that is in direct continuity with the plantar fascia and the tendon of the plantaris. It appears to have no immediate attachment to the os calcis other than that derived from the plantaris tendon. From the tendon of the flexor tibialis, however, it derives some aponeurotic extensions. Four small fleshy bellies emerge from these aponeurotic attachments and they give rise to four slender tendons that pass to the four postaxial digits. Their attachments to the digits are those characteristic of the perforated flexors.

Fig. 50.



Deep muscles of posterior aspect of left leg. P=popliteus. TP=tibialis posterior.

*MM. Lumbricales* are four in number, arising in the typical manner from the tendons of the flexor tibialis and destined for the four postaxial digits.

*MM. Interossei* are crowded into the very narrow intervals between the metatarsal bones and are exceedingly difficult to define, but they appear to be normal in number and arrangement and act as abductors and adductors of the digits about the axis of the third digit.

The intrinsic muscles of the pes agree in disposition with the description of Cunningham for *Phascogale* and differ only from those in *Dasyurus*, as described by MacCormick, in that the dual nature of the lumbricales to which he draws attention could not be verified in any specimen of *Dasyercus*.

#### Abdominal Muscles.

*M. Rectus abdominis* is marked by a series of intermuscular intersections, of which the first may be regarded as the potential division between the rectus abdominis and *M. Rectus thoracis*. The rectus thoracis or *M. Sternalis* is attached as far forwards as the first rib.

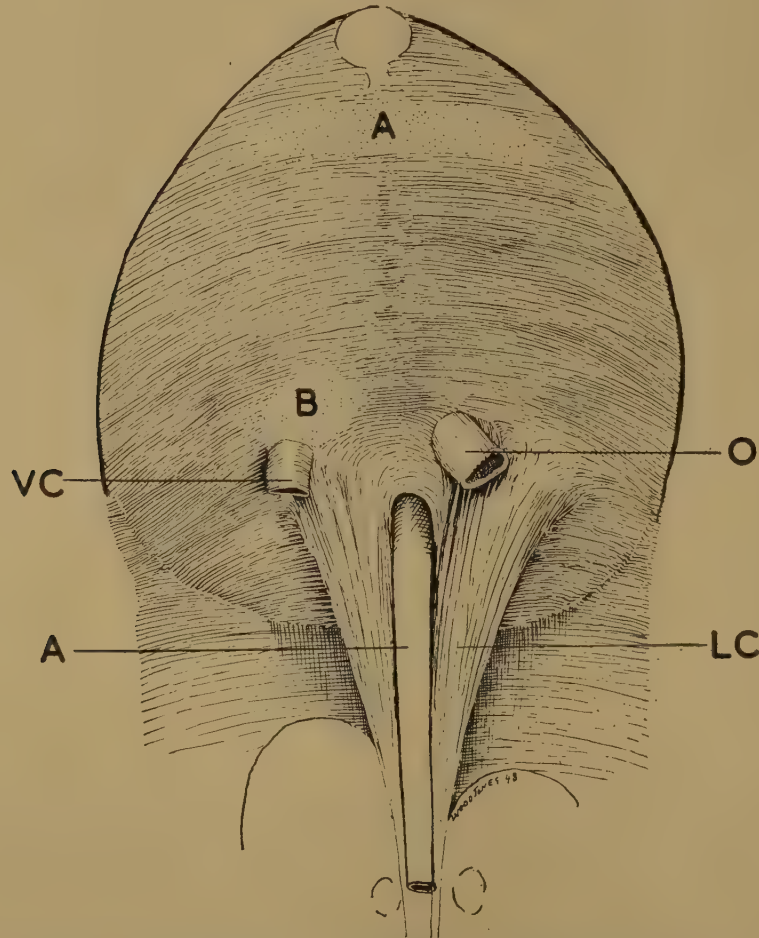


The *M. Pyramidalis* is, as usual in marsupials, a large muscle attached to the marsupial bone and passing over the rectus as far forwards as the costal margin.

The *MM. Obliquus abdominis externus* and *internus* are normal in their attachments and disposition.

*M. Transversus abdominis* is remarkable chiefly on account of its manifest continuity with the muscular diaphragm.

Fig. 51.



The abdominal surface of the diaphragm. A and B=the membranous portions. O=oesophagus. VC=vena cava. A=aorta. LC=left crus.

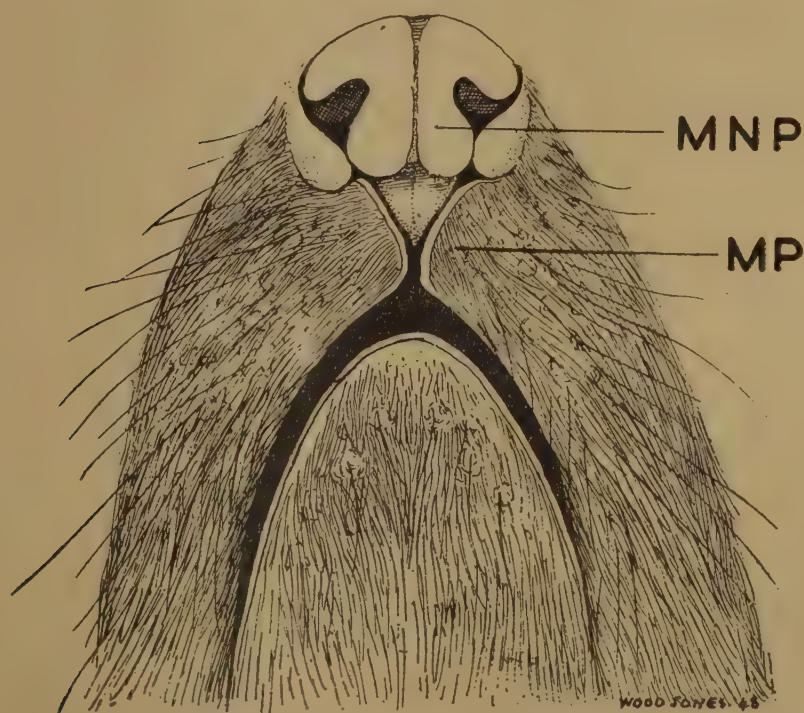
The *Diaphragm* (see fig. 51) is noteworthy in that it is a simple muscular sheet which, though having two somewhat variable aponeurotic areas, has no central or cordiform tendon. The aponeurotic areas consist of a small ventral thinning situated behind the ziphisternal fibres and a larger dorsal area in the neighbourhood of the orifice for the inferior vena cava. The muscular fibres, which are in manifest continuity with those of the transversus abdominis, run, for the most part, transversely across the body. The crura, though well developed, are singularly aloof from the general fabric of the diaphragm and they form practically no interlacement with the transverse fibres, nor make any considerable contribution to the

musculature of the septum itself. The oesophageal aperture receives almost no encircling fibres from either crus. The two crura are of practically equal size, the left-sided crus being somewhat the larger, if any disparity is present. The vertebral attachments extend distally immediately adjacent to the medial aspects of the kidneys and adrenal bodies. The aorta enters the abdominal cavity between the two crura, behind the general transversus sheet that constitutes the diaphragm.

#### APPARATUS DIGESTORIUS.

The *Rhinarium* and *Lips* (see figs. 2 and 52 and Pl. II, fig. 3). The rhinarium is naked, brownish pink in colour and finely tessellated by shallow surface furrows. The mesial nasal processes are marked by a slight furrow in the mid line above the upper lip and their fused lower ends pass as a narrow naked area between the maxillary processes to the interspace between the two upper median incisors.

Fig. 52.



The rhinarium and lips. MNP=mesial nasal process. MP=maxillary process.

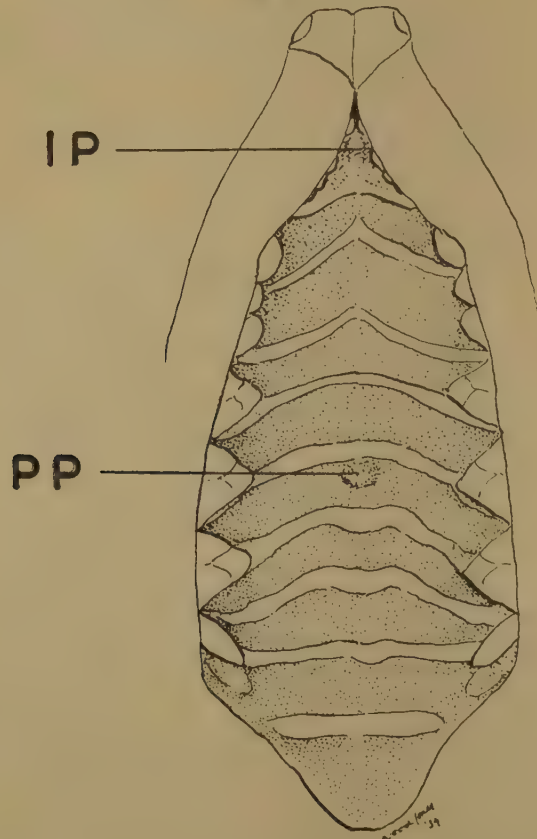
In this manner they form the basis of a frenulum labii superioris. The lateral nasal processes form the lateral margins of the comma-shaped nostrils and are naked on their medial surface. The maxillary processes complete the upper lip and they are covered by fine hair continuous with that clothing the mystacial area. The cutaneomucous area of the upper lip is small and linear and its buccal surface, though studded with small glandular elevations, gives rise to no papillae. The lower lip has only a linear naked cutaneous margin and, like the upper lip, has no visible papillae or cornified processes on its buccal aspect. The buccal



surface of the cheeks is also devoid of papillae, though buccal glands produce slight elevations on its mucous membrane.

The *Palate* (see fig. 53). The mucous membrane covering the hard palate is sculptured by the typical palatal rugae. In *Dasyercus* there are nine transverse rugae passing completely across the convexity of the hard palate. Of these rugae the second and third, which originate behind the canine and second premolar respectively, are in the form of double crescents, concave forwards; the fourth, fifth, sixth and seventh are simple arcuate ridges with the convexity directed forwards. The eighth and ninth are practically straight bars: the ninth being

Fig. 53.



The hard palate showing the distribution of the palatal rugae. IP=incisive papilla. PP=palatine papilla situated behind the fifth palatal bar.  $\times 4$ .

altogether behind the last molar tooth. A somewhat diffuse incisive papilla is situated anterior to the first bar. A well-defined papilla is present behind the fifth bar and smaller, scattered, tubercles between all the posterior bars. In *Dasyuroides*, according to Carlsson, the defined papilla lies behind the eighth bar, which seems anomalous and does not appear to be verified in her figure 14. In *Dasyurus* two lie behind the fifth, sixth and seventh. Those behind the sixth and seventh are almost confluent in the mid line.

The soft palate stretches from the hinder end of the hard palate. It is devoid of transverse rugae and exhibits a smooth mucous membrane directed towards

the buccal and pharyngeal cavities. The soft palate exhibits the typical condition present in primitive mammals, for it becomes continuous with the posterior wall of the pharynx and *has no free posterior border*, other than the anterior margin of the hiatus nasopharyngeus. It forms a complete septum from the roof of the oral cavity to the posterior wall of the pharynx and the upper part of the oesophagus, save where a median aperture, the *hiatus nasopharyngeus*, permits the orifice of the larynx to pass upwards into the nasal chambers. It is not, in *Dasyercus*, that there is merely an "intranarial epiglottis", but the orifice of the larynx is protruded through the hiatus nasopharyngeus and retained normally in the nasal chambers. With the exception of this orifice there is no other communication between the nasal chambers and the buccopharynx. The buccal cavity, therefore, communicates with the oesophagus only by two lateral channels running upon either side of the larynx beneath the soft palate and above the posterior part of the tongue and the floor of the mouth. It is obvious, from the examination of a number of specimens, that the orifice of the larynx may be withdrawn through the aperture in the soft palate and may take up a buccal rather than a nasal position; but apparently the normal condition is that the laryngeal orifice is thrust through the aperture into the posterior part of the nasal chamber. *Dasyercus* is perhaps unique in the fact that the larynx remains in the nasal chamber after death and can only be dislodged by use of some little force.

The *Tongue* (see figs. 54 and 55) is elongated and fusiform. It is indented by eight transverse grooves impressed upon it by the rugae of the palate. Over the free tip, as far back as the third transverse groove, the tongue shows a well-marked median furrow. This furrow is more extensive in *Dasyurus*, where it is present over the major part of the length of the tongue, but is said by Carlsson to be absent in *Dasyuroides*. An apical fringe of horny fungiform papillae is present at the extreme tip and elsewhere on the dorsum these papillae are scattered in most irregular fashion. In one specimen a total of 55 papillae was recognizable and of these 30 were on the right side and 25 on the left. Three large and well-defined circumvallate papillae are present, their number and disposition being identical in *Dasyercus*, *Dasyuroides* and *Dasyurus*.

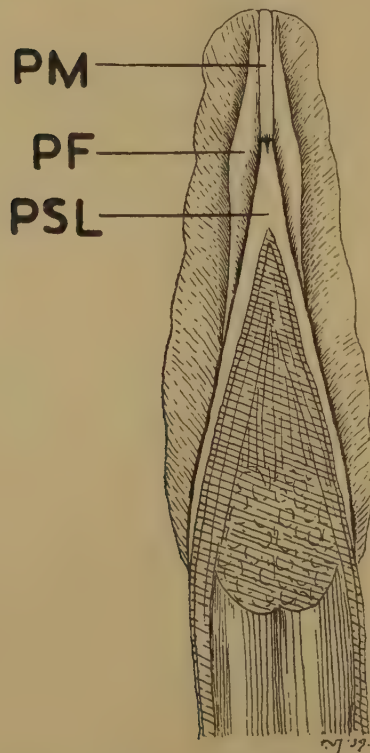
The plica sublingualis is in its typical primitive form and terminates in a bifid distal extremity. The plica fimbriata is unserrated along its lateral free edges and is present as a smooth horny fold extending from the free tip of the tongue to behind the mid point of its length. The plica mediana is particularly well developed and constitutes a rounded median elevation over the whole of the free portion of the tongue. In all respects these structures resemble those present in *Dasyurus*, but they differ from *Dasyuroides*, as described and figured by Carlsson, in that the conspicuous plica mediana is omitted altogether in her account, although the statement is made that "the tongue of *Dasyuroides* resembles that of *Dasyurus*".

*Salivary Glands* (see figs. 56 and 57). Since there is some considerable confusion in the literature, it seems best to describe the *conchal gland* in connection with the salivary glands, although it belongs to an altogether different system. The conchal gland is a large sebaceous gland associated with the concha of the ear, first described in *Dasyurus maugei* (= *D. viverrinus* = *D. quoll*) by R. H. Burne (*J. Anat. Physiol.*, 43, 312, 1909), and in *Dasyercus* it is well developed. It is



closely applied to the posterior and lower aspect of the concha at its junction with the cartilaginous external auditory meatus. It is firm and compact in consistency and its surface is smooth and yellowish white in colour. In its gross shape it is very much like the quadrant of an orange wrapped round the back of the concha, to which it is closely adherent by reason of the crypt-like orifices by which the secretion is discharged into the cavity of the external ear. It is not mentioned as being present in Carlsson's description of *Dasyuroides*, but from the statement that the parotid "surrounds the anterior, posterior and inferior aspects of the external ear" it seems possible that the gland was mistakenly included in the general

Fig. 54.



The underside of the tongue showing the sublingual structures.  $\times 4$ . PM=plica mediana.  
PF=plica fimbriata. PSL=plica sublingualis.

Fig. 55.

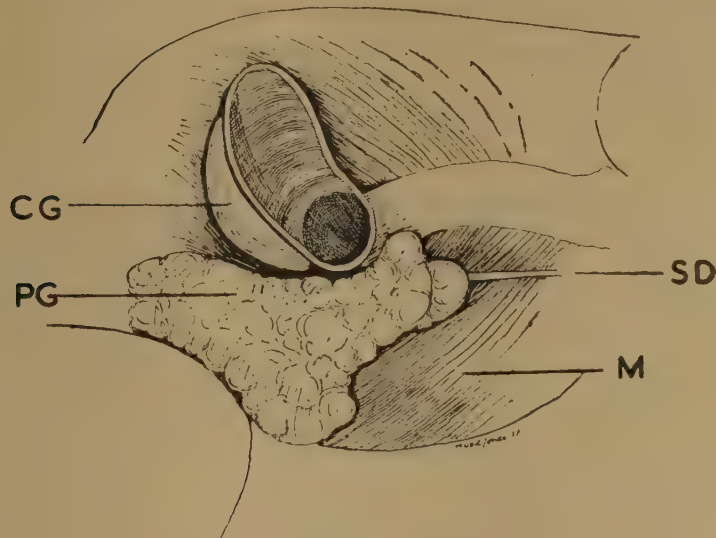


Dorsal surface of the tongue.  $\times 4$ .  
CP=circumvallate papillae.

system of the parotid complex. From the parotid it is, however, readily distinguished by its dense and compact structure and by the fact that it is definitely enclosed in its own well-differentiated capsule.

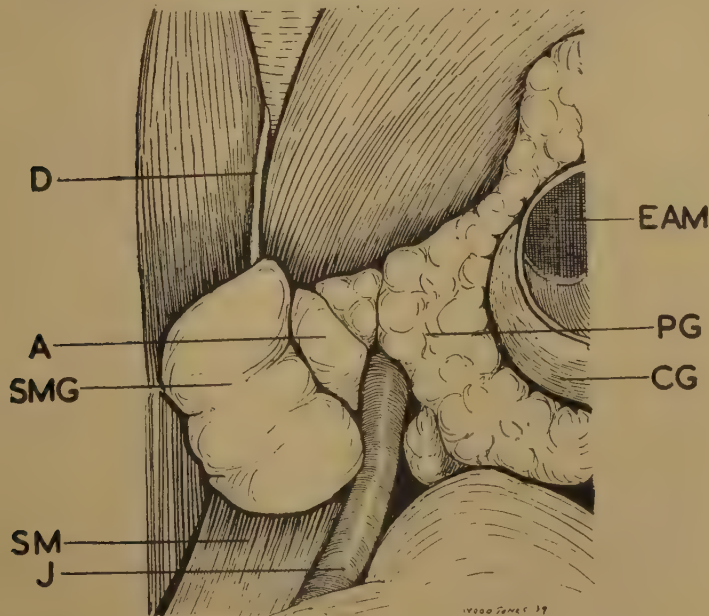
The parotid complex consists of a large and diffuse glandular mass extending over the side of the face and front of the neck and stretching from the zygoma to the root of the neck and shoulder region. The facial portion lies on the masseter in front of the ear and from its most anterior extension, which is not definitely separated from the main mass as a *socia parotidis* (glans parotis accessoria), the duct emerges, to run its usual course across the masseter and end by piercing the buccinator muscle.

Fig. 56.



Right side of the face with the concha cut from the external auditory meatus. CG=conchal gland. PG=parotid gland with SD its duct passing over the masseter muscle M.

Fig. 57.



Left side of the neck dissected to show the salivary glands. The concha has been cut from the external auditory meatus EAM. CG=conchal gland. PG=parotid gland. SMG=submandibular gland, with D its duct. A=accessory retrolingual gland. SM=sterno-mastoid. J=internal jugular vein. EAM=external auditory meatus.

The facial portion also extends behind the external auditory meatus, separated from it by the discrete conchal gland, and passing back to the shoulder region. From the facial portion of the gland an extension passes ventrally to the front of the neck. Here it crosses the internal jugular vein and has some irregular



extensions, more or less separated from the main mass, lying upon both sides of the jugular. The most posterior extension of the cervical mass lies lateral to the jugular and sterno-mastoid and reaches as far back as the pectoralis-deltoid muscle complex of the shoulder. Although Owen regarded the parotid gland of *Dasyurus* as being small, such is hardly the case in most of the specimens that I have examined.

The *submaxillary (submandibular) gland* (see fig. 57) rests mainly on the upper end of the sterno-mastoid muscle, filling the interspace between it and the masseteric fibres sweeping over the bulla. The gland lies altogether medial to the jugular. From the parotid and its cervical outliers with which it comes in contact, it is distinguished by its less lobulated and more compact structure. On its mesial aspect it passes on to the digastric and sterno-hyoid muscles. The duct of the gland (Wharton's duct) passes from the anterior aspect of the main mass and lies in the interspace between the masseter laterally and the digastric medially. It then passes between the ramus of the mandible and the anterior belly of the digastric and has the usual termination in the floor of the buccal cavity beneath the tongue.

There are the usual salivary glands lying on the buccal surface of the mylohyoid beneath the tongue and these are obviously those to which Carlsson, in *Dasyuroides*, gives the names *sublingual* and *retrolingual*. In addition to these glands situated in the buccal cavity, there is a gland mass appearing on the surface of the submandibular region between the subaural portions of the parotid and the normal submandibular gland (see fig. 57). This small lobe is discrete and confined to its own fibrous capsule and it differs in naked-eye appearance from the submandibular on its medial and the parotid on its lateral side. It is situated superficially immediately medial to the internal jugular vein and histologically (see fig. 58) is apparently a part of the sublingual complex separated from the retrolingual gland by the intervention of the mylohyoid muscle. Its ducts apparently join the duct of the submandibular gland as well as opening independently into the floor of the buccal cavity. In fig. 57 it is indicated as the *accessory retrolingual gland*. By W. C. Mackenzie it was apparently diagnosed as a lymphatic gland. According to Owen the sublingual gland is absent in *Dasyurus*; but this is not correct so far as my examinations of this form are concerned.

*Alimentary tract.* The *stomach*, when empty (see fig. 59), is almost globular in shape. The organ is thick-walled and the demarcation of the pylorus from the duodenum is well marked. The mucous membrane is for the most part arranged in a series of deep longitudinal folds. On the ventral (lesser curvature) aspect of the stomach the oesophageal and the pyloric orifices are close together; so that the "lesser curvature" is almost obliterated, the interval being occupied by a gastric lobule of the pancreas. The fundus extends as far to the left (dorsal) aspect of the oesophagus as the pylorus does to the right. When dilated (see fig. 60) the fundus enlarges and becomes dependent on the left side of the abdominal cavity. In this enlargement a well-marked incisura is developed on the greater curvature and the whole organ assumes an almost bilocular form.

The *duodenum* is a wide-bored tube forming a well-marked duodenal curve which is occupied by the thin-spread multilobed pancreas. The remainder of the intestine is extremely simple: it is suspended on a simple mesentery and is coiled mainly on the right side of the abdominal cavity. There is no definite *caecum* but

in some specimens a change of bore in the bowel and a change in intestinal contents would almost seem to mark the site of a physiological change in intestinal function. The dilated portion immediately following the constriction lies above on the right side, immediately below the right lateral lobe of the liver and from this dilation

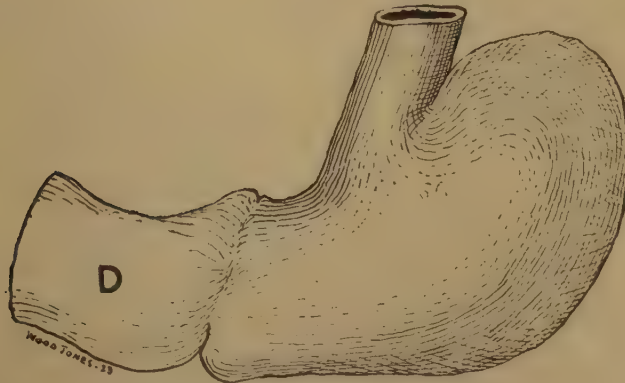
Fig. 58.



Section of the submandibular gland B and the accessory retrolingual gland A.

the gut passes in the median line to the rectum. The length of the intestine in a spirit-preserved adult was 234 mm. from pylorus to anus: the head and body length of the specimen was 160 mm. In another specimen of head and body length 135 mm., the intestine measured 230 mm. The intestinal canal is, therefore,

Fig. 59.

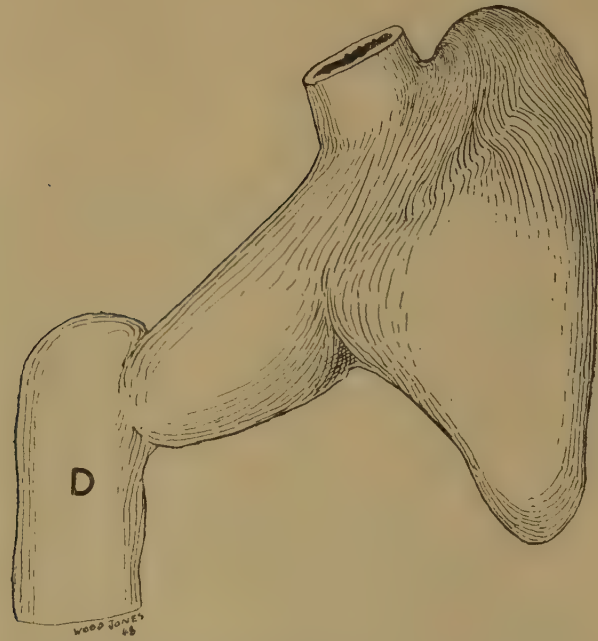


Form of the empty and contracted stomach. D=duodenum.

only about one and a half times the head and body length; and so is considerably less than the ratio recorded by Carlsson for *Dasyuroides* (1 : 2.53), or for *Phascogale* (1 : 2.64). The whole alimentary canal resembles that of *Antechinomys* as described by Beddard.



Fig. 60.



Form of the distended stomach. D=duodenum.

Fig. 61.

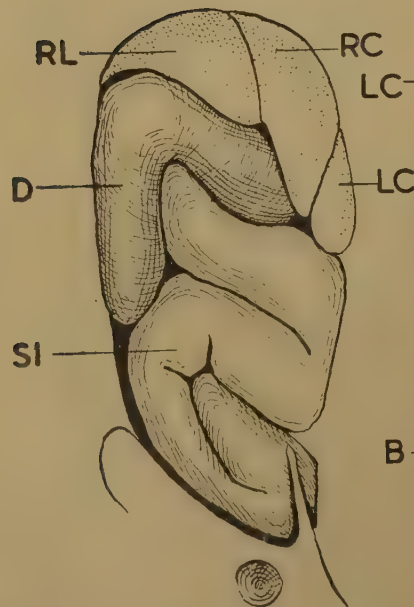


Fig. 62.

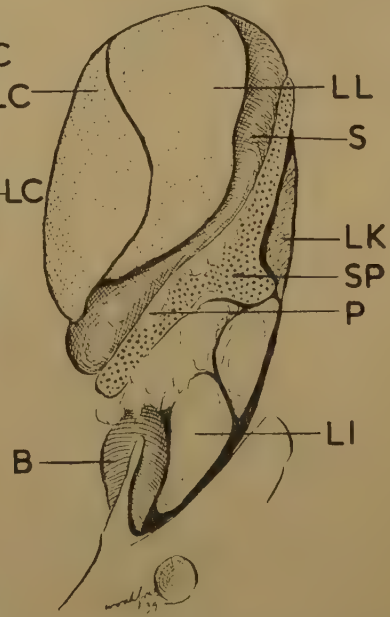
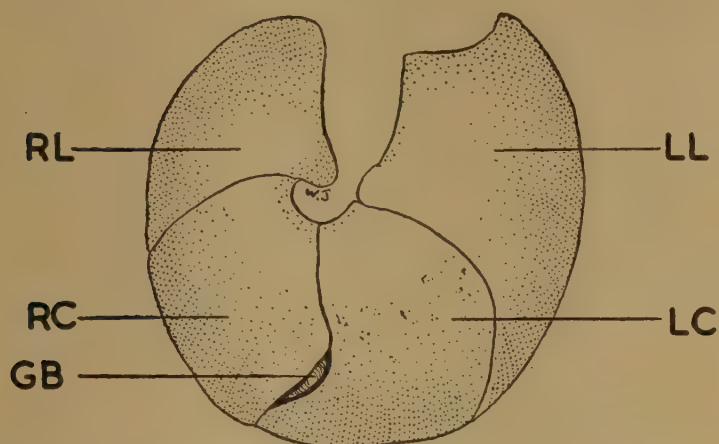


Fig. 61. General abdominal viscera seen from the right. Fig. 62. As seen from the left.  
 RL=right lateral. RC=right central. LC=left central. LL=left lateral bone of the liver.  
 S=stomach. D=duodenum. SI=small intestine. LI=large intestine. SP=spleen.  
 P=pancreas. LK=left kidney. B=bladder.

The *Liver* (see figs. 63–67) consists of four distinct lobes in addition to the Spigelian lobe and its caudate extremity. These lobes consist of :

(1) the right lateral, which forms a somewhat inconsiderable portion of the diaphragmatic aspect of the organ but which is prolonged downwards and gives

Fig. 63.

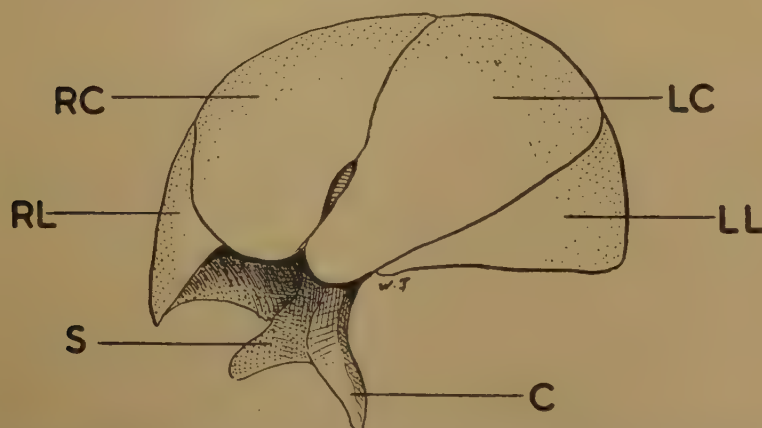


The liver : diaphragmatic surface. GB=gall bladder. RL=right lateral lobe. RC=right central lobe. LL=left lateral lobe. LC=left central lobe.

rise to the prominent and somewhat complicated lobus Spigelii with its elongated prismatic caudate extension ;

(2) the right central lobe which contributes largely to the right anterior aspect of the organ and which is deeply excavated for the reception of the gall bladder,

Fig. 64.



The liver : ventral surface. S=Spigelian lobe. C=caudate process. Other lettering as in fig. 63.

which is visible both from the abdominal and diaphragmatic aspects of the liver ;

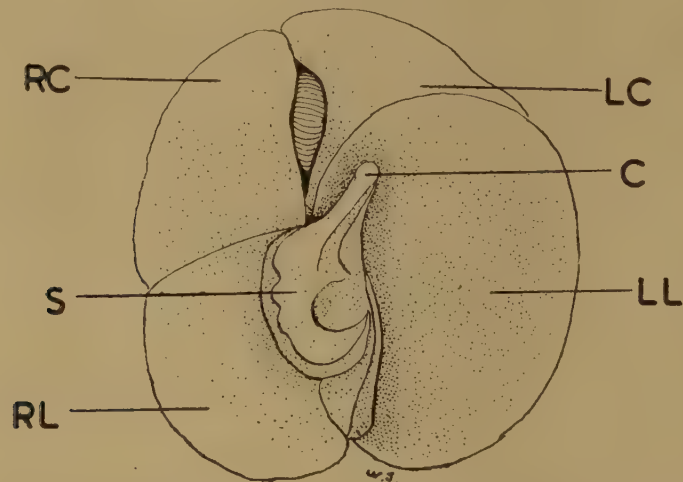
(3) the left central lobe reciprocally indented by the gall bladder below and forming the major portion of the anterior aspect of the organ ;

(4) the large, tongue-shaped left lateral lobe.



There is no trace of a round ligament. Carlsson's description of the liver of *Dasyuroides* is somewhat difficult to follow. According to her account, it is divided into three sections, of which the left central is so small that it "can hardly be seen in diaphragmatic aspect". The statement that the "not very well marked" Spigelian lobe arises from the left lateral lobe would seem to be definitely erroneous. Her figure of the liver (figure 16) is not helpful in this respect. The liver of *Dasyercus* may be said to be of a generalized marsupial type.

Fig. 65.



The liver: abdominal surface. Lettering as in figs. 63 and 64.

The *Pancreas* (see fig. 62) is of the typical diffuse lobulated form. Its duct opens into the duodenal loop close to the opening of the bile duct.

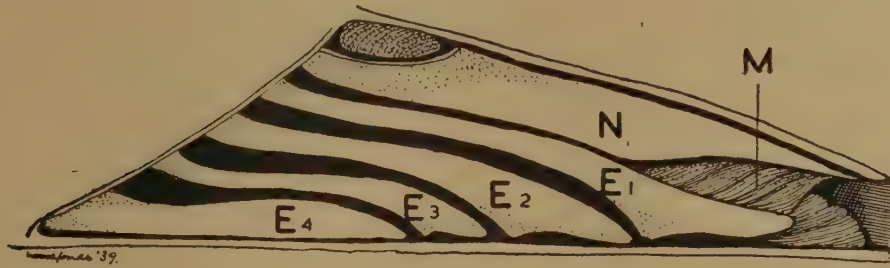
The *Spleen* (see fig. 62) is composed of three elongated lobes. The superior lobe passes upwards between the greater curvature of the stomach and the lateral margin of the left kidney. The posterior lobe passes backwards to the lower pole of the left kidney and the lower lobe passes downwards on the left side of the abdomen, so that its lowest extremity extends downwards to the anterior aspect of the bladder. From this lobe the omentum passes over the coils of intestine in the lower left compartment of the abdomen. In one specimen a small accessory spleen lay in the omentum at the tip of the descending lobe.

#### APPARATUS RESPIRATORIOUS.

The *nasal chambers* are elongated in harmony with the projected muzzle. The nasal septum, dividing the right from the left chamber, extends only over the anterior portion of the nasal respiratory tract; a posterior undivided recess existing behind the separated nasal chambers. It is into this posterior, undivided recess that the larynx is thrust through the hiatus nasopharyngeus, under normal circumstances. The lateral walls of the nasal chambers proper give rise to the *turbinate bones*. These, as is usual in marsupials, consist of one nasoturbinal, four ethmoturbinals and one maxilloturbinal (see fig. 66). The *nasoturbinal* is elongated, stretching the whole length of the upper part of the nasal chamber and

ending anteriorly either as a tapering (as in fig. 66) or as an enlarged extremity. In some specimens this extremity is wholly or partially detached from the main mass of the nasoturbinal. The fold is simple, no secondary sculpturing being present. The *maxilloturbinal* is normal, its anterior extremity being complicated by secondary foldings. The four *ethmoturbinals* are large scrolls which, although appearing simple as viewed on the lateral wall of the nasal chamber, are complicated in their deeper

Fig. 66.



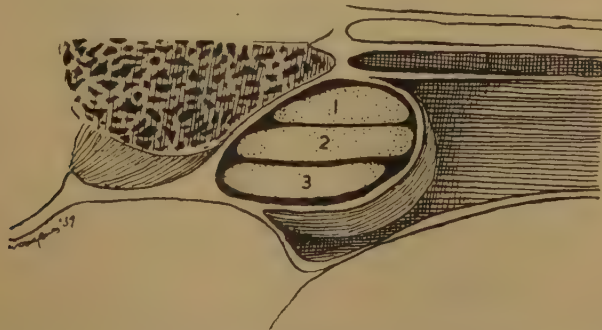
The lateral wall of the left nasal chamber showing the turbinated bones. N=nasoturbinal.

M=maxilloturbinal. E=ethmoturbinals 1, 2, 3, 4.

extensions in the upper part of the cavity. These complicated deep foldings are contained in a separate recess of the nasal chamber which lies in the upper and back part of the cavity separated from the large cribriform plate of the ethmoid by the thin, anterior wall of the anterior fossa of the skull (see fig. 67).

Carlsson makes no mention of the conchae in *Dasyuroides*; but the condition in *Dasyercus* agrees with that in *Dasyurus* and *Phascogale*.

Fig. 67.

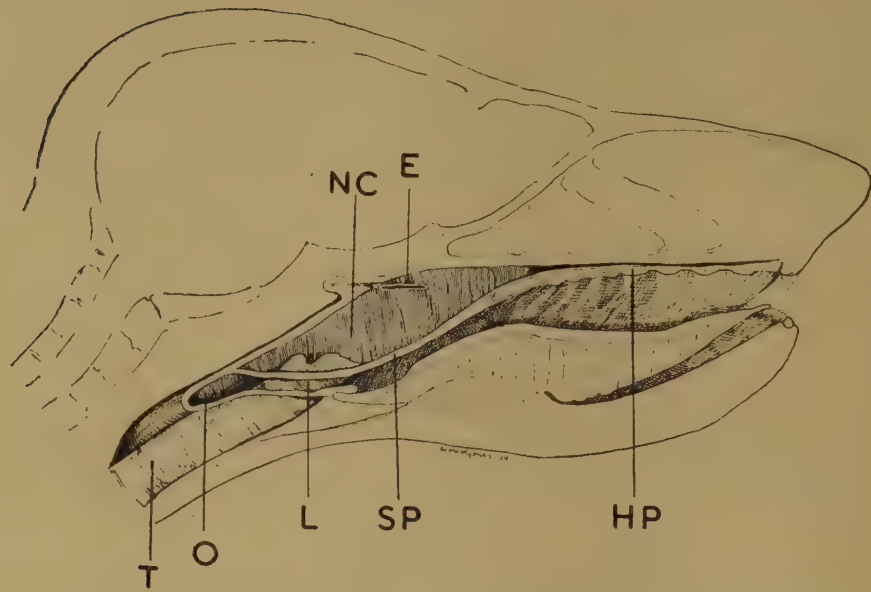


The hind end of the right nasal chamber opened from above; showing the deep portions of the upper ethmoturbinals in the ethmoidal recess.

*The Intranarial Larynx.*—In the majority of specimens, both young and adult, the larynx remained in the nasal chambers after death (see fig. 68). In most cases the larynx, protruded into the posterior recess of the nasal chamber, was tightly grasped by fibres of the palato-pharyngeus (see fig. 69). Its position is evidently controlled by the palato-laryngeus muscle which passes, posterior to the palato-glossus, from the posterior end of the soft palate to the lateral aspect of the thyroid

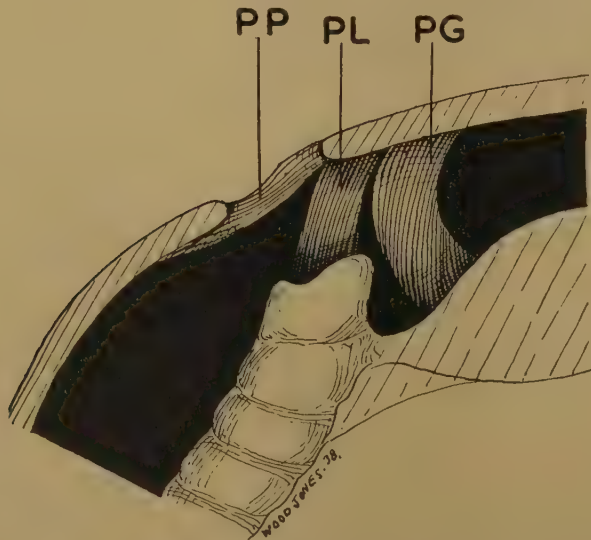


Fig. 68.



Sagittal section of the head immediately to the right of the middle line showing the larynx *in situ* in the nasal chamber. E=orifice of Eustachian tube. HP=hard palate. SP=soft palate. L=larynx passing through the hiatus nasopharyngeus. O=oesophagus. T=trachea. NC=posterior recess of the nasal chamber.

Fig. 69.

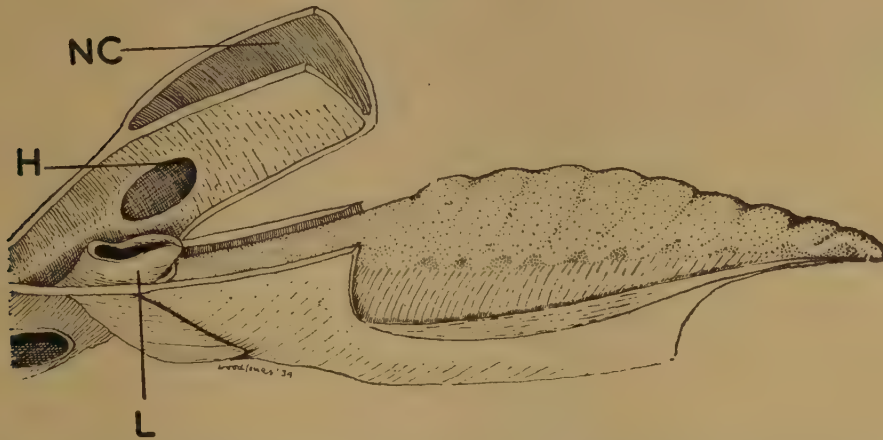


Semi-diagrammatic drawing of the larynx and palate to show the disposition of the palatal muscles in relation to the hiatus nasopharyngeus. PG=palatoglossus. PL=palatolaryngeus. PP=palatopharyngeus, surrounding the hiatus nasopharyngeus.

cartilage and the overlying hyoid bone. On withdrawing the larynx from the hiatus nasopharyngeus, the site of the grasping fibres of the palatopharyngeus is usually marked by a constriction of the soft tissues covering the proximal part of the laryngeal cartilages (see fig. 70).

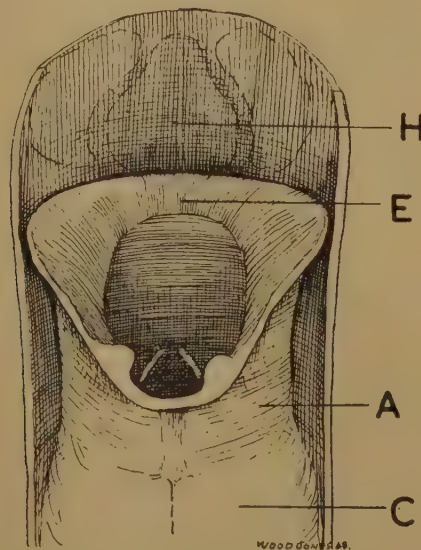
The copula portion of the peculiarly shaped *Hyoid* is so intimately related to the laryngeal cartilages that it is most conveniently described in connection with the respiratory apparatus. It is remarkable in its form and consists of five elements (see figs. 71 and 72). Of these cartilaginous elements one is situated in the mid line

Fig. 70.



Larynx, palate, tongue, etc. dissected from the right side, showing the larynx removed from the hiatus nasopharyngeus. NC=posterior recess of nasal chambers. H=hiatus nasopharyngeus. L=larynx.

Fig. 71.

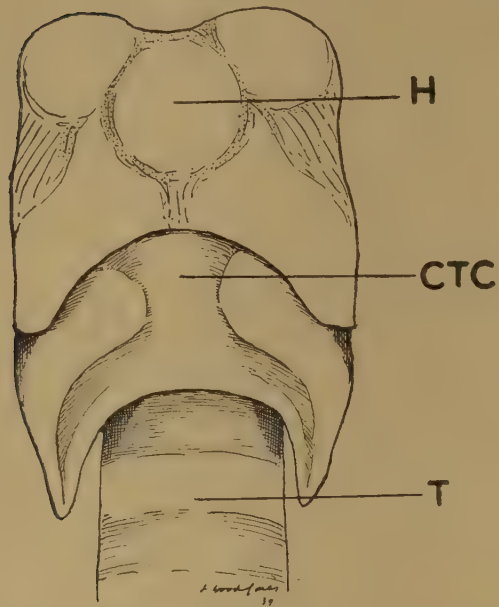


Dorsal aspect of the larynx with the mucous membrane intact.  $\times 9$ . H=hyoid. E=epiglottis. A=arytenoid. C=cricoid.

and two are disposed upon either side of it in a cephalic and two in a caudal direction. The central mass (*basihyal*) consists of a flat plaque which remains cartilaginous even in old individuals. This plaque is of a general rounded outline with usually a narrowing at its cephalic extremity (fig. 71), so that the whole figure

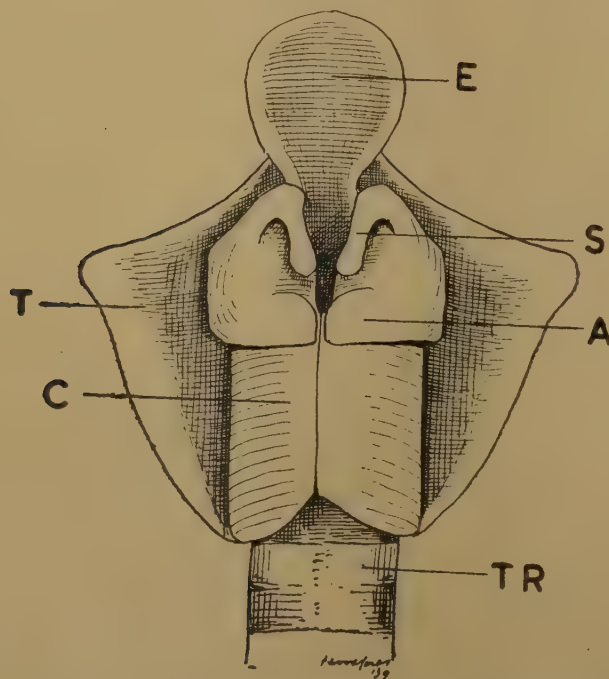


Fig. 72.



Ventral aspect of the hyoid and larynx. H=hyoid. CTC=cricothyroid complex. T=trachea.

Fig. 73.

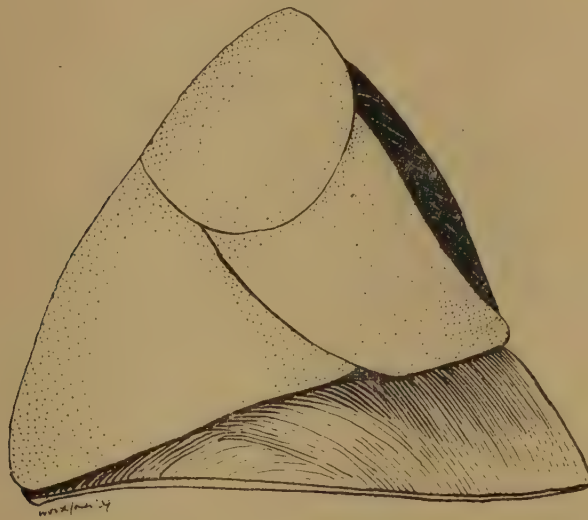


Dorsal aspect of the laryngeal cartilages. E=epiglottic cartilage. S=cartilage of Santorini. A=arytenoid. T=thyroid. C=cricoid. TR=trachea.

tends to be piriform. The bilateral cephalic cartilaginous plates (*ceratohyals*) are separated from the median mass by a slight membranous interval and are roughly crescentic in outline, their medial concave borders being shaped in harmony with

the convex margins of the central mass. The caudal masses (*thyrohyals*) are larger and are elongated in a caudal direction laterally overlying the ventral surface of the thyroid cartilage and articulating ultimately with the cricoid element of the cricothyroid complex. This peculiar, broad, flattened hyoid is present in *Dasyurus*, the same five separate elements being present but, in the adults of this genus, they are completely ossified. Fairly free movement is permitted around the articulation between the posterior extensions of the hyoid with the cricothyroid complex; the movement being of the same kind as that which takes place between the thyroid and cricoid in the *Monodelphia*. No cartilaginous connection exists between the ceratohyals and the tympanic region of the skull, but a fibrous cord connects them and the point of attachment of the styloid muscles.

Fig. 74.



The lungs and heart from the right side. The upper, middle and lower lobes of the right lung are visible.

The *Epiglottis* is like that of the other *Dasyuridae* in being broad and prominent with a thin rolled free border. The epiglottic cartilage is extremely thin and flexible and supports only the central part of the whole extent of the fold of mucous membrane. In shape, the cartilage may be likened to a battledore, the handle of which is attached at the ventral angle of the thyroid cartilage (see fig. 73). The laryngeal cartilages differ from those of *Dasyurus* in minor details only.

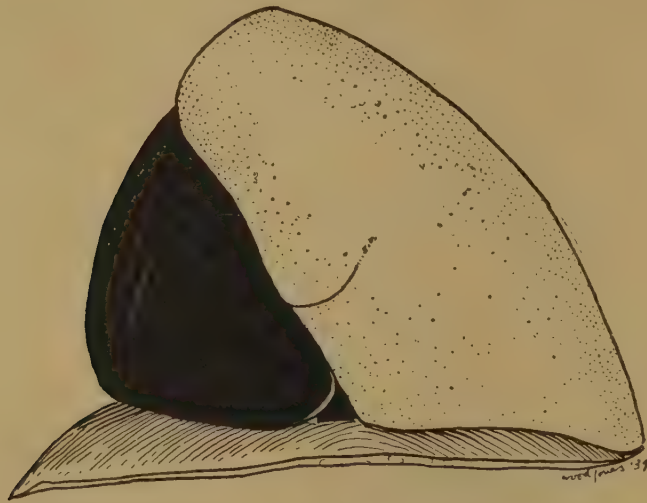
The *Arytenoid Cartilages* (see fig. 73) are relatively enormous and are connected with the large recurved and hook-like cartilages of Santorini—*corniculate cartilages*. The muscular processes of the arytenoids are large and prominent bosses situated on the mesial aspect of the cartilages, just above their articulation with the cricoid.

The *Cricoid* and *Thyroid Cartilages* are conjoined into a cricothyroid complex, as is usual in the *Dasyuridae*. Despite the complete fusion of the two elements their individuality is plainly indicated by surface markings on the external aspect of the larynx. The cricoid, unlike that of *Dasyurus*, is completely closed dorsally, a



median groove marking the area of junction. The thyroid is bossed in the mid line on its ventral aspect and passes backwards as two posterior cornua which, at their hinder end, merge with the posterior extremities of the cricoid. The lateral portions of the thyroid articulate directly with the posterior prolongations of the hyoid. The dilator muscle passes from the cricoid to the muscular process on the arytenoid. The sphincter passes from the cricothyroid complex laterally and becomes continuous across the mid line, on the posterior aspect of the arytenoids, with its fellow of the opposite side. No cartilage could be detected in the mid line junction of the two muscles, although its presence has been described in other members of the *Dasyuridae*.

Fig. 75.



The heart and lungs from the left side. The small incisura indenting the anterior margin of the otherwise undivided left lung is shown.

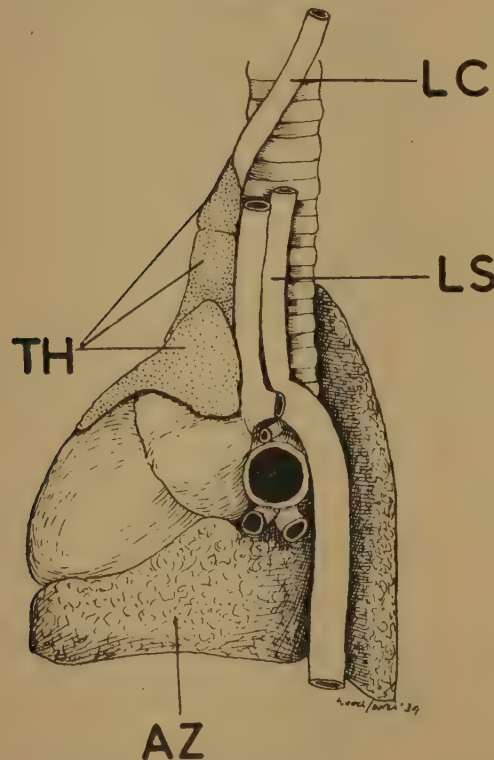
The *Trachea* consists of twenty rings, all of which are incomplete over a small area on the dorsal aspect.

The *Lungs*.—The right lung has four lobes : an upper, middle and lower and an azygos lobe (see fig. 74). The left is considerably smaller than the right and only shows a partial subdivision into upper and lower lobes. The subdivision is present only on the anterior margin ; the posterior portion showing no surface indication of any separation of the two lobes (see fig. 75). Carlsson describes the right lung of *Dasyuroides* as “divided into two lobes, and an additional lobus azygos” : but this seems most unlikely to be correct, since apparently all the members of the *Dasyuridae* possess three lobes in addition to the azygos lobe. In *Dasyuroides* Carlsson noted no particular separation of two lobes in the left lung and, if no such partial subdivision is actually present, *Dasyuroides* resembles *Dasyurus* in which the left lung is undivided, whereas *Dasyercus* resembles *Phascogale*.

## ANGIOLOGY.

The *Heart* (see figs. 76 and 77) shows no features of note and conforms to the classical descriptions of the cardiac anatomy of the marsupials as given by Owen. The aortic arch is of a broad type and the left subclavian artery arises a considerable distance to the left of the carotid trunk. The right subclavian, although arising in common with the carotid trunk, is given off so low down as to be almost an aortic branch. In some cases its independence of the common trunk is even more pronounced than in the specimen illustrated in fig. 77. In this variation it differs somewhat from the typical marsupial plan and even from that present in the *Dasyures*. In *Dasyuroides* Carlsson describes "a single trunk" which "issues

Fig. 76.



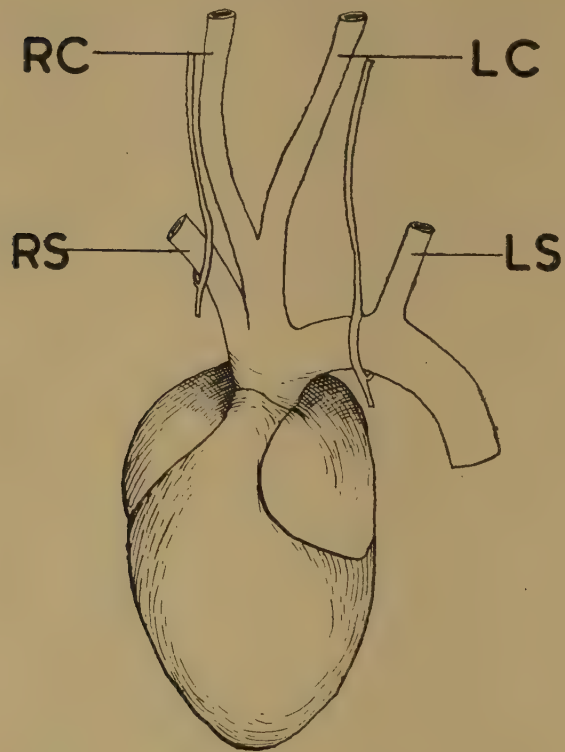
The heart and great vessels from the left side with the left lung removed.  $\times 4$ . LC=left carotid.

LS=left subclavian. AZ=azygos lobe of the right lung. TH=thymic tissue.

from the aortic arch, gives off the right subclavian and later divides into the right and left carotid arteries". This description would apply perhaps to the specimen illustrated in fig. 77, but, without qualification, could not be said to define the condition present in all examples of *Dasyurus*. The two common carotid arteries arise by bifurcation of the common trunk and run their usual course in the neck. The main interest of the carotid system lies in the internal carotid and its method of entering the cranial cavity. On the ectocranial aspect of the base of the skull, between the caudal extension of the pterygoid plate and the sphenoidal element of the auditory bulla, is a deep depression, from the bottom of which two foramina lead into the cranial cavity. From the postero-lateral foramen issues the third

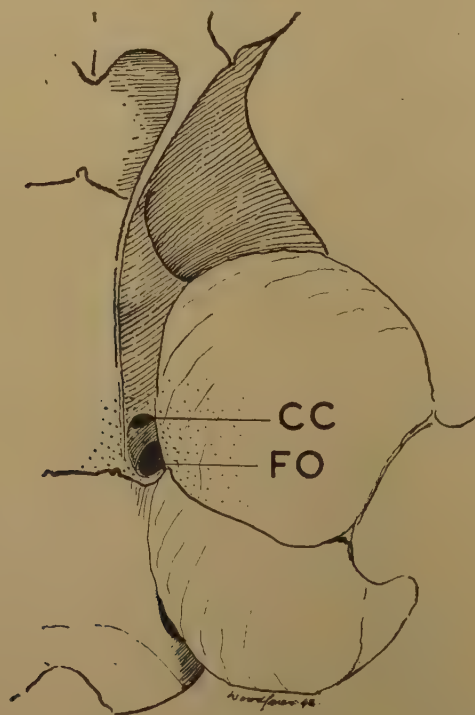


Fig. 77.



The heart and great vessels. Anterior aspect.  $\times 4$ . RS=right subclavian. RC=right carotid. LC=left carotid. LS=left subclavian. The vagus nerves are shown in relation to the great vessels.

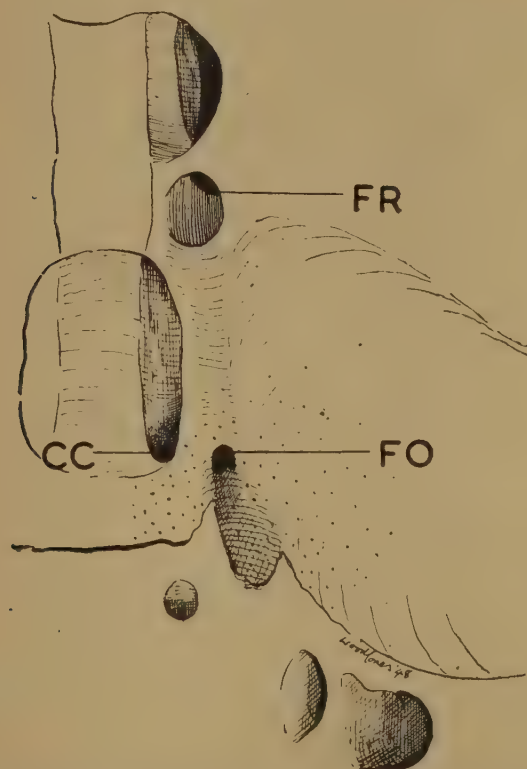
Fig. 78.



Ectocranial aspect of the base of the skull showing the bulla region and the carotid canal (CC) in relation to the foramen ovale (FO) at the caudal end of the sphenoid.

division of the trigeminal nerve and through the antero-mesial foramen the internal carotid enters the skull. The foramen ovale and the carotid canal therefore share a common orifice on the ectocranial aspect on the base of the skull and this common orifice is situated in the *sphenoid* bone. Moreover, the carotid canal pierces the sphenoid anterior to the foramen of emergence of the third division of the fifth cranial nerve (see fig. 78). Passing into the skull the two foramina lead into canals that divorce themselves from one another and the carotid canal enters the cranial cavity immediately to the medial side of the foramen ovale. From the point of entrance of the carotid canal a groove runs forwards on the body of the sphenoid

Fig. 79.



Endocranial aspect of the base of the skull showing the carotid canal (CC) in relation to the foramen ovale. (FO) at the caudal end of the sphenoid. FR=foramen rotundum.

(see fig. 79). In this groove the artery is lodged and its course and distribution are of the normal marsupial pattern. The passage of the carotid canal through the sphenoid, instead of the petrous temporal, is a marsupial character and as such was noted by Flower. The earlier writers on marsupial anatomy appear, for the most part, to have overlooked the great taxonomic importance of the fact that whereas in *Monodelphia* the carotids enter the skull through the petrous temporal and in relation to the tympanic cavity, in members of the *Didelphia* the entrance is through the sphenoid, unrelated to the cavity of the tympanum.

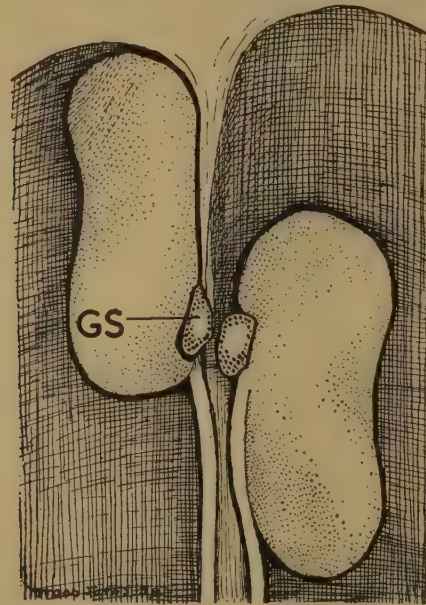
No feature of special importance is to be noted in the distribution of the peripheral vessels—arterial or venous—in other parts of the body.



## APPARATUS UROGENITALS.

The *Kidneys*, though generally symmetrical in size and shape, are markedly asymmetrical in position. The right kidney is always situated considerably further forwards in the abdominal cavity than is its fellow of the opposite side. In general, the lower pole of the right kidney is on approximately the same level as the hilum of the left kidney and this relation is maintained no matter what the form of the kidney may be in the individual animal. In shape they are remarkably variable in different individuals, for although in some specimens they are what may be termed "human" in form, in others they are considerably more elongated

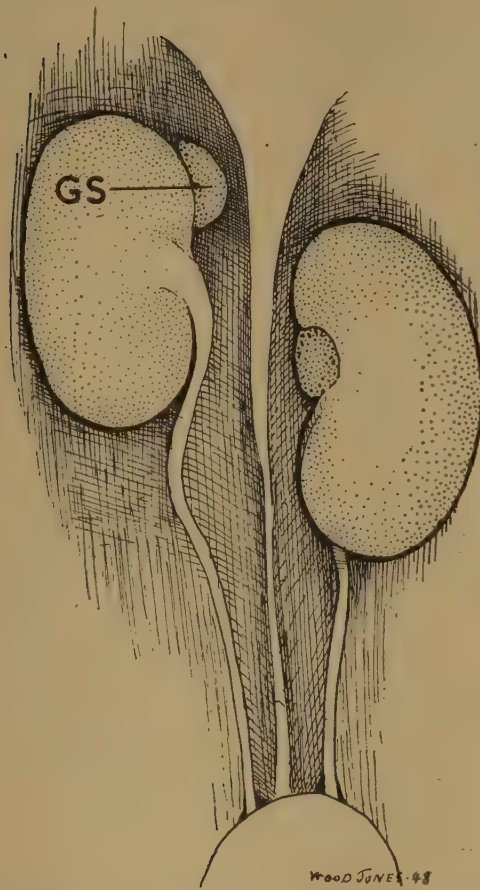
Fig. 80.



Position and form of the kidneys and glandulae suprarenales in specimen A, an immature female.  
GS=suprarenal gland of right side.

and less curved in general outline. The two specimens illustrated in figs. 80 and 81 are respectively an immature female and an adult male, but the gross variation in form appears to be independent of age or sex. Intermediate forms between these two extremes were met with and it would seem that, whatever the individual form, the two kidneys are always of the same type. The lateral margins may be convex, almost straight or even concave. The length of the kidneys may markedly exceed their breadth or be only slightly greater. In this feature, as in the origin of the aortic branches and many other characters, *Dasycercus* appears to manifest individual variations in excess of the usual expectation within the limits of a species. The upper pole of the right kidney is situated immediately below the right dome of the diaphragm in intimate relation with the right lateral and Spigelian lobes of the liver. The left kidney is displaced in a caudal direction by the intervention of the fundus of the stomach and the spleen. The two organs, and the ureters, are

Fig. 81.



Position and form of the kidneys and glandulae suprarenales in specimen B, an adult male.  
GS=suprarenal gland of right side.

Fig. 82.



Section of kidney and ureter showing the single renal papilla projecting into the pelvis of the ureter.



separated in the mid line by the intervention of the linear origin of the simple mesentery of the intestinal canal.

In structure the kidney is extremely simple, there being a single, undivided medullary mass that culminates in a single elongated papilla. This papilla is remarkable for its great length and for its extension into the sinus of the ureter (see fig. 82). It is produced as a long nipple-shaped process contained within the wide pelvis of the kidney and projecting some distance into the upper part of the ureter. Such a development of the renal medulla would seem to be a characteristic feature of the more generalized polyprotodonts, for it is present to a somewhat lesser degree in *Myrmecobius* and *Dasyurus* and Owen reported it in *Didelphis*.

The *Ureters* run a somewhat tortuous course on the posterior abdominal wall, that on the right side being necessarily considerably longer than its fellow. In the female they pass ventrally, in the typical marsupial fashion, by running to the base of the bladder between the two lateral vaginae. In the male they come into association with the vasa deferentia as the latter enter the prostatic urethra.

The *Bladder* differs remarkably in its distended and contracted states. When distended it is spherical and capacious and rises some 18 mm. above the symphysis pubis (see fig. 83). When contracted it shrinks, even in the fully adult male, to a small mass considerably less than the upper part of the prostatic urethra in diameter (see fig. 91).

The proximal portion of the *urethra* anterior to the formation of the long urogenital sinus in the female, is a simple muscular tube. In the male it is encircled by the prostate gland immediately below the neck of the bladder and will be described with the male reproductive system.

#### REPRODUCTIVE SYSTEM OF THE FEMALE.

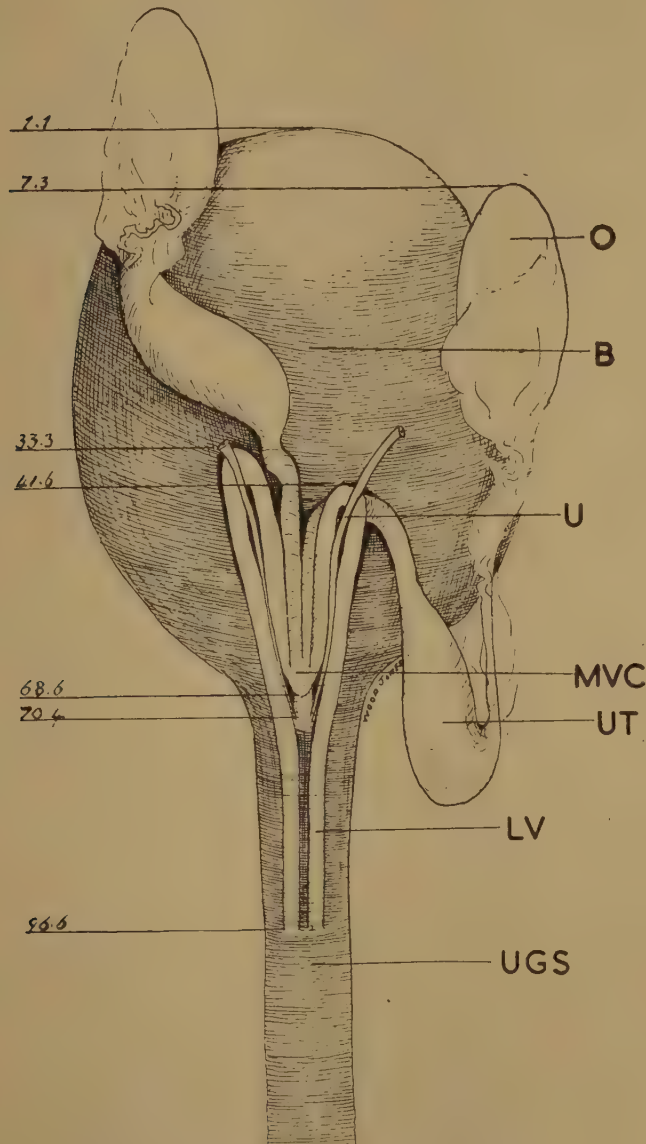
The following of the tortuous course of the various passages of the female internal genitalia proved so difficult a task by gross anatomical methods that serial sections were made of the whole reproductive tract of one young and two adult females. From the sections of one adult female, mounted on the first 96 slides, the figure (reproduced as fig. 83) was reconstructed. The uterus and ovary of the right side of the excised specimen had dropped to a lower level than those of the left and the resulting reconstruction therefore shows a lack of symmetry that was not present in the undisturbed state.

The *Ovary* is oval in outline but little flattened in a dorsi-ventral direction. Its peritoneal relations are normal. Upon the surface of the ovary the minute, tortuous *Fallopian tube* courses towards the caudal pole and there opens into the thick-walled and well differentiated uterus. The *uteri* themselves are fusiform in shape and are about the same length as the long axis of the ovaries. The *uteri* pass into the uterine canals, from which they are distinctly differentiated by the change in bore and the thickness of the muscular walls.

The *median vaginal canals* pass, closely approximated, behind the base of the bladder to terminate in the median vaginal cul-de-sac, the common caudal pole of which is closely adherent to the posterior aspect of the bladder medial to the terminal portions of the ureters. From the cul-de-sac the tubes pass abruptly in a cephalic direction as the *lateral vaginal canals*, which loop around the ureters

to pass caudally once more on the base of the bladder, lateral to the ureters. The ureters pass ventral and terminate medially to the lateral vaginal canals just below the caudal limits of the median vaginal cul-de-sac, the lower parts of which terminate in a mass of cellular tissue just cephalic to the ureteric openings

Fig. 83.



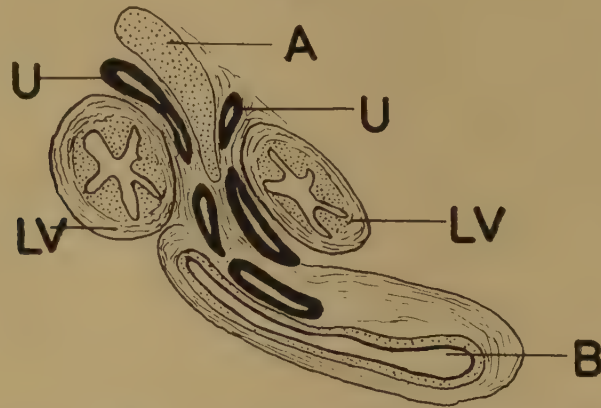
Reproductive system of an adult female. The figure is a reconstruction from serial sections (slides 1-120) and only the upper portion of the long urogenital sinus is shown. B=posterior aspect of bladder. O=ovary. U=ureter. UT=uterus. MVC=median vaginal cul-de-sac. LV=lateral vagina. UGS=urogenital sinus.

into the bladder (see fig. 84). The lateral vaginal canals, having looped over the ureters, pass caudally, laterally to them behind the base of the bladder and so to the posterior aspect of the urethra. In the upper part of their course below the termination of the ureters they are free of the tissues of the urethral wall, but



lower down they become closely approximated and incorporated in a common tissue strand (see fig. 85). During this stage of their course their lumina become reduced to mere cellular interspaces which subsequently become recanalized before they open into the urogenital sinus (see fig. 86). The *urogenital* sinus runs a comparatively long direct course before opening into the cloaca.

Fig. 84.

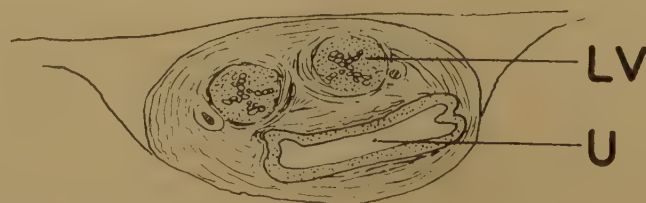


Section 4, slide 70, showing the passage of the ureters between the two lateral vaginæ to open into urinary tract. A=tissue in which the medial vaginal cul-de-sac ends. U=ureter. B=bladder LV=lateral vagina.

The female reproductive system of *Dasycercus* is in general conformity with the condition present in other polyprotodonts and bears a very definite likeness to that of *Myrmecobius* described by J. P. Hill.

From *Dasyurus*, as described by Pearson, *Dasycercus* differs in the absence of the elongated "vaginal necks" intervening between the uteri and the median vaginal canals. But it resembles that genus in the great length of the urogenital sinus and the shortness of the urethra. Like *Dasyurus*, *Dasycercus* possesses

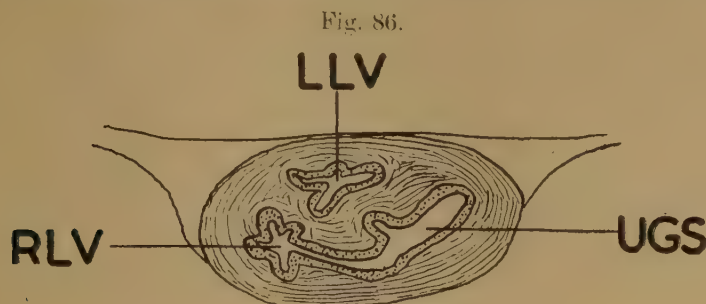
Fig. 85.



Section 4, slide 81. Showing the lateral vaginæ incorporated in the wall of the urogenital cord and with their lumina occluded. LV=lateral vagina. U=urethra.

small median vaginal culs-de-sac which do not reach the uro-genital sinus and which are divided by a septum that is apparently permanent throughout life. It is worthy of note that the specimen from which the reconstruction (fig. 83) was made was an adult female known to have produced young. The period of gestation is unknown, but there is good evidence for assuming that it is limited to a very small number of days.

The *Mammary Area* (see fig. 87 and Pl. I, fig. 2).—At no time of life, or in any phase of the reproductive cycle, is there any sort of marsupium or pouch, although there is always present a definite, specialized suprapubic mammary area. This is area oval in form with its long axis directed cranio-caudally. Very commonly the



Section 6, slide 96, showing the junction of the right lateral vagina with the urogenital sinus.  
RLV=right lateral vagina. LLV=left lateral vagina. UGS=urogenital sinus.

area is indented in the middle line at its cranial extremity, giving rise to an almost heart-shaped contour. The area is surrounded by a fairly well-marked ridge separating it from the surrounding abdominal region. It is also rendered distinct by the fact that it is clothed by minute white hairs different altogether in texture

Fig. 87.



Mammary area and nipples of an adult female that had recently suckled eight young.

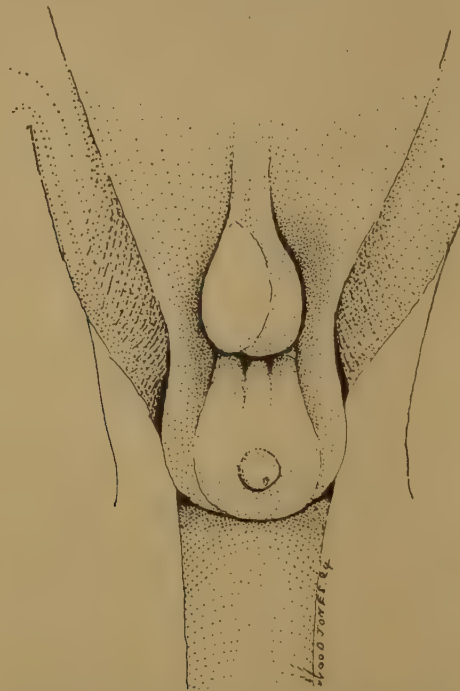
from the general hair-covering of the lower abdominal area. The number of nipples varies from six to eight, the larger number being by far the commoner. The nipples are simple papillae in the quiescent state, but become considerably elongated and conical in form during the period of suckling. In captivity the average litter is seven, but eight is by no means uncommon.



## REPRODUCTIVE SYSTEM OF THE MALE.

The scrotum is in the usual marsupial suprapubic site. In the adult male its diameter is some 12 mm. and it shows little or no evidence of bilateral structure. A definite fraenulum, however, runs caudally from the posterior aspect of the scrotum towards the cloacal orifice : but its identity as a definite anatomical structure ceases a very short distance behind the scrotum and no raphe is to be detected over the remainder of the perineal area (see figs. 88 and 89). The scrotum is clothed by very short and rather stiff hairs, the tips of which are all directed caudally. The deep surface of the scrotal skin and the whole of the tunica vaginalis are deeply pigmented : the whole coverings of the testis being intense black, in marked contrast to the pale colour of the testis itself. It is attached

Fig. 88.



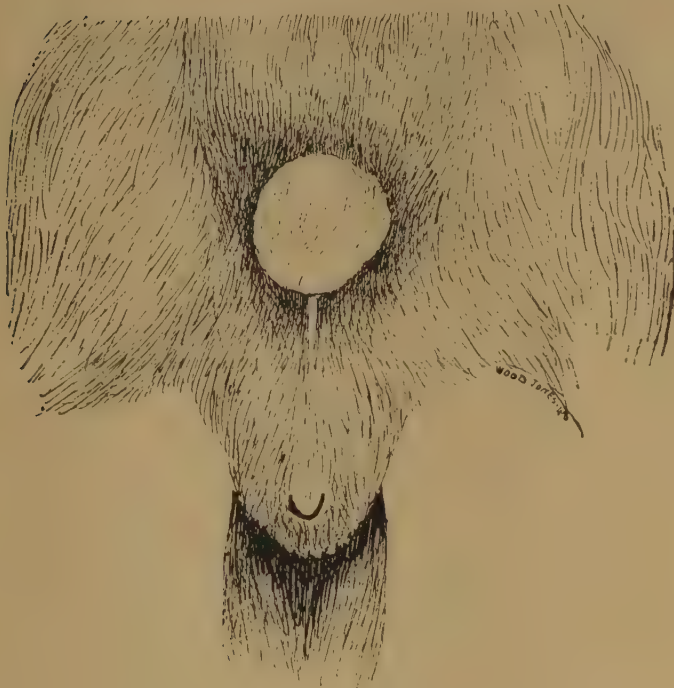
External genitalia of an immature male.

to the anterior abdominal wall by an extremely slender pedicle in which the vessels and the vasa deferentia run. The septum scroti is thick and contains a large quantity of fat. The approximated aspects of the two testes are flattened against the septum scroti.

The *Testis* measures some 7 mm. in its long axis and the epididymis, extending both cranially and caudally beyond the limits of the testis, is 10 mm. from caput to cauda. Both caput and cauda are equally well developed and the slender vas deferens arising at the caudal pole runs its usual course along the medial aspect of the testis and so to the scrotal peduncle and the anterior abdominal wall and inguinal canal (see fig. 91).

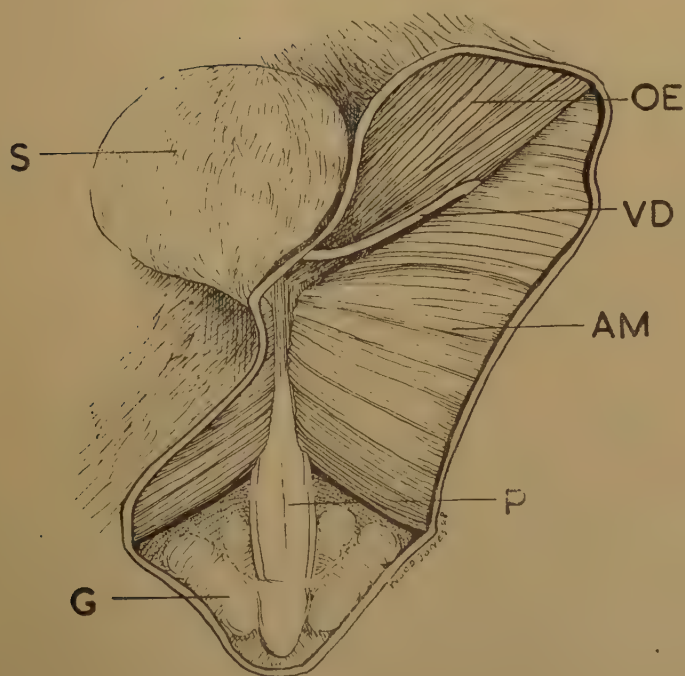
The testes occupy their extra-abdominal subcutaneous scrotal site at a very early stage in development. In the naked male suckling, of which a section is shown

Fig. 89.



External genitalia of an adult male.

Fig. 90.



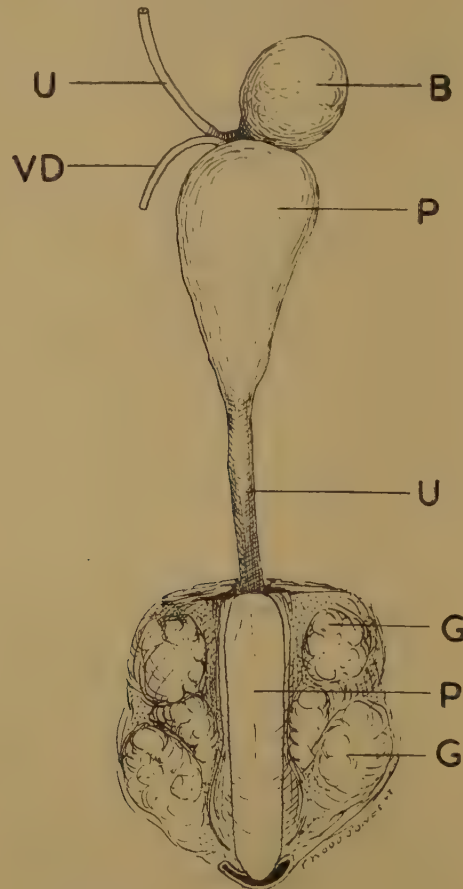
External genitalia of an adult male. Superficial dissection. OE=obliquus externus abdominis. VD=vas deferens. AM=adductor muscles of the thigh. P=body of the penis. G=bulbo-urethrales glands. S=scrotum.



in fig. 92, the testes are already in their adult position in the extra-abdominal area scroti, although no scrotal pouch is developed. The dependent scrotal sac is prominent before the period of suckling comes to an end (see fig. 88).

The *Vasa deferentia* terminate by opening into the urethra immediately distal to the well-developed sphincter vesicae. No dilation of their terminal ends is apparent in their extra-urethral course, even in the adult male, and no specialized vesiculae seminales are present. At their point of entry into the prostatic portion of the urethra no specialized uterus masculinus or prostatic utricle is present.

Fig. 91.



Urogenital system of an adult male. B=bladder. P=prostatic urethra. U=urethra.

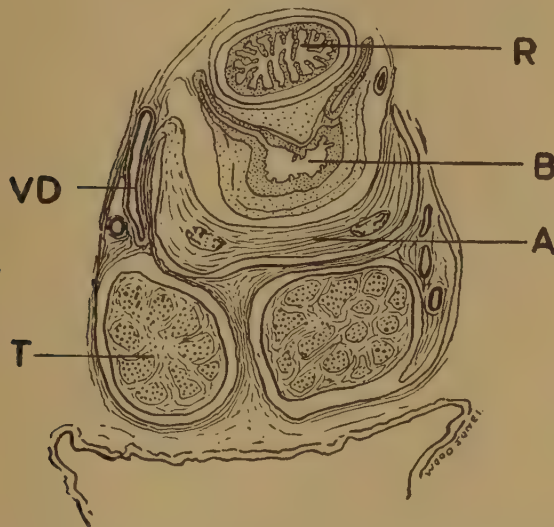
VD=vas deferens. P=body of penis. G=glandulae bulbo-urethrales.

The *Prostate* constitutes an elongated fusiform gland that surrounds the intra-pelvic portion of the urethra in rather more than its proximal half. In proportion to the size of the animal the gland is relatively enormous (see fig. 91). The urethra passes through the midst of the gland, which surrounds it on all sides, there being as much prostatic tissue ventral to the canal as there is on its dorsal aspect (see Pl. II, fig. 4). The distal portion of the intra-pelvic urethra, which constitutes rather less of the whole intra-pelvic course than does the prostatic portion, consists of a simple muscular tube devoid of glandular thickening. The extra-pelvic or penile portion of the urethra consists of the complicated "bulb" and distal, penile

parts together with the aggregated masses of the *glandulae bulbo-urethrales* (Cowper's glands).

The penile portion proper consists of the erectile bodies with their associated muscular masses, the ischio-cavernosi and bulbo-cavernosi. Added to these muscles are the well-developed retractores penis and the ventral unpaired levator penis. The body of the penis remains single to the extremity of the glans, which is always visible at the anterior margin of the cloaca in the undisturbed condition of the parts. In the glans being undivided, even at its tip, *Dasyrcerus* differs from *Myrmecobius*.

Fig. 92.



Section of the lower part of the abdomen in a male embryo. R=rectum. B=bladder into which the ureters are opening. A=muscles of the anterior abdominal wall with the included suprapubic bones. T=testes. VD=vas deferens.

The *Glandulae bulbo-urethrales* are extremely large and their size is increased by their thick covering of muscle. Three separate glands are present upon each side of the bulb of the penis. Of these three the most dorsal pair is by far the largest. The other two pairs of glands, situated more proximally, are smaller as actual glandular masses and possess a thinner muscular coat. All six glands possess short ducts which open into the bulbar portion of the urethra.

The whole male genital tract, like that of the female, bears a strong general likeness to that of *Myrmecobius* as described by Fordham. The most striking difference is the undivided condition of the glans in *Dasyrcerus* in which the armature of the penis is considerably less developed than it is in *Myrmecobius*.

#### THE CENTRAL NERVOUS SYSTEM.

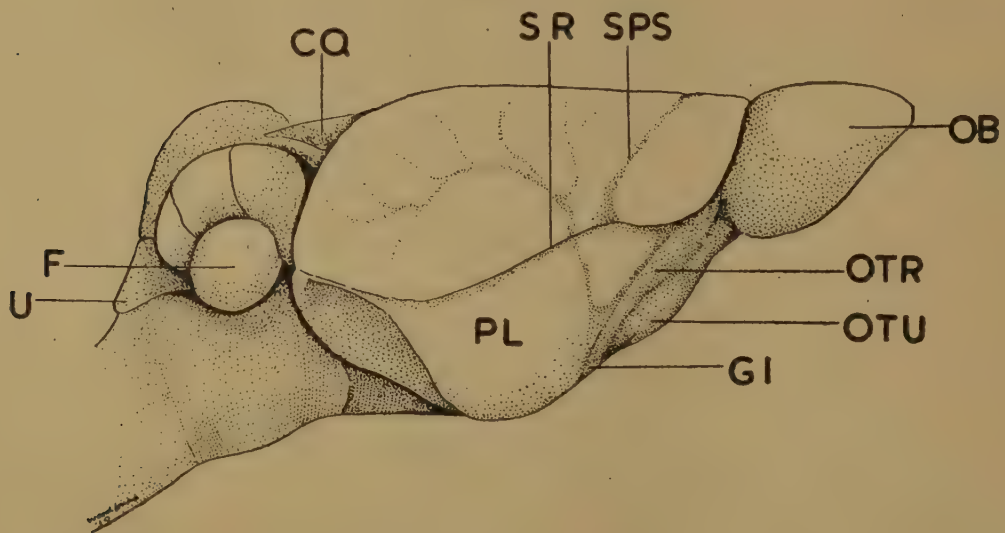
The *Brain*, in conformity with the shape of the cranium, is broad and somewhat flattened in its dorsi-ventral axis. The total length of the brain, including the cerebellum, is about  $1\frac{1}{2}$  times its greatest breadth, whereas in *Dasyurus* the length is almost double the breadth. In proportion to the size of the animal the brain is



large. Relying on linear measurements alone the brain of *Dasycercus* is more than twice as large as that of *Dasyurus* when brain and body dimensions are compared.

The *Pallium*, like that of all small Dasyures, is practically devoid of surface fissuration. A shallow furrow at the anterior quarter of the length of the pallium is constant enough to be regarded as a normal topographical feature. The lower limits of this furrow become practically confluent with the anterior portion of the rhinal fissure and it may probably be regarded as a minimal manifestation of the *presylvian sulcus* (see figs. 93 and 95). Further back on the lateral surface of the pallium are other, fainter and inconstant furrows, but these are obviously vascular markings and cannot be regarded as normal features of pallial architecture. On the medial surface of the pallium *Dasycercus*, like the other smaller members of

Fig. 93.

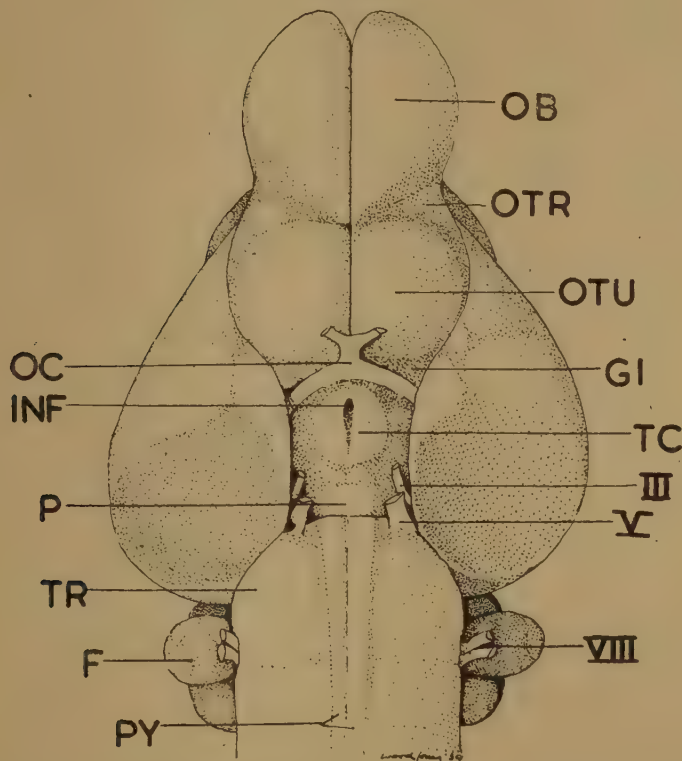


Right lateral aspect of the brain of a large adult male.  $\times 4.5$ . OB=olfactory bulb. OTR=olfactory tract. OTU=olfactory tubercle. GI="gyrus intermedius". PL=pyriform lobe. U=uvula. F=flocculus. CQ=corpora quadrigemina. SR=sulcus rhinalis. SPS=presylvian sulcus.

the Dasyuridae, has no trace of any part of the calcarine complex. With the exception therefore of the very shallow, but constant, presylvian sulcus, the pallium remains unmarked by sulci or gyri. Upon the lateral aspect of the brain the pallium constitutes more than half of the surface of the cerebral hemisphere: in this regard the pallium of *Dasycercus* exceeds that of most of the other dasyurids in which the pyriform lobe is relatively larger. The pallium is very distinctly marked off from the pyriform lobe by the *rhinal sulcus* (see fig. 93). This fissure runs backwards along the lateral margin of the hemisphere from between the anterior pole of the pallium and the pedicle of the olfactory bulb to the posterior pole of the hemisphere. The anterior portion of the sulcus runs with a slight convexity downwards; the intermediate portion is convex above and the posterior extremity again bends upwards to the caudal pole of the hemisphere (see fig. 93). The rhinal sulcus separates the pallium above from the well-developed pyriform

lobe below. The constituent parts of the rhinencephalon are all well developed, as is the case with all the Dasyuridae. The *olfactory bulbs* are large, but are relatively less well developed than in such nocturnal forms as *Sarcophilus*. Observations upon the living animal would seem to indicate that during its day-light hunting activities the olfactory sense was by no means so dominantly important, as it undoubtedly is in the more strictly crepuscular and nocturnal members of the Dasyuridae. The connections of the olfactory bulbs with the rest of the cerebral hemispheres are plainly indicated by surface sculpturing of the brain stem.

Fig. 94.



Basal aspect of the brain of an adult female.  $\times 4.5$ . OB=olfactory bulb. OTR=olfactory tract. OTU=olfactory tubercle. GI="gyrus intermedius". TC=tuber cinereum. III, V and VIII=third, fifth and eighth cranial nerves. PY=pyramids. F=flocculus. TR=trapezoid body. P=pons varolii. INF=infundibulum. OC=optic chiasma.

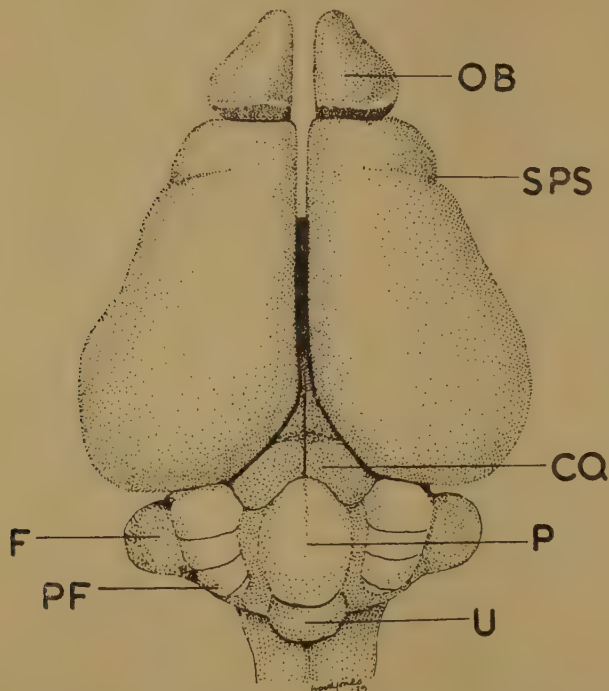
The *Olfactory Tract* runs caudally between, first the pallium and the olfactory bulbs, and then between the pyriform lobe and the olfactory tubercle. The tract loses its identity caudally just anterior to the optic tract and posterior to the olfactory tubercle (see figs. 93 and 94). The caudal extremity of the visible sculpturing of the tract is situated in a small tubercle—the "gyrus intermedius" of Retzius—for which Elliot Smith proposed the name tubercle of the olfactory tract. Since Elliot Smith's term is liable to create confusion with the olfactory tubercle itself, this swelling is here referred to by the name given to it by Retzius.

The *Olfactory Tubercle* itself, though large, is by no means so disproportionately



developed as it is in many other small marsupials, both polyprotodont and diprotodont. It is conspicuous on the lateral and basal aspects of the hemisphere as a rounded tumescent area of the brain lying mesial to the olfactory tract and occupying the whole base of the brain from the olfactory bulbs in front to the optic tract behind. On the medial surface of the hemisphere the olfactory tubercle lies below the precommissural area of the cortex and immediately in front of the commissures and lamina terminalis (see fig. 96). Towards the caudal pole of the brain the *Gyrus dentatus* (fascia dentata) makes a wide sweep from the precommissural area of the olfactory peduncle dorsally and caudally and then passes in an arcuate course downwards and forwards to the temporal pole of the hemisphere and

Fig. 95.



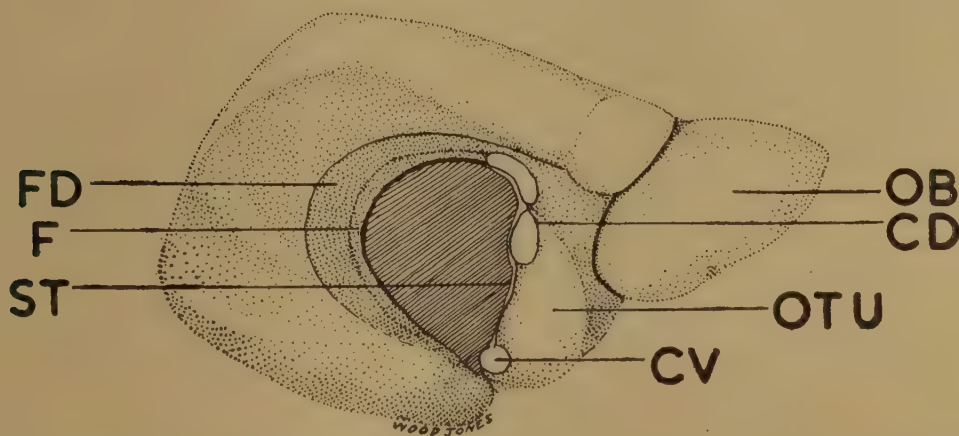
Dorsal aspect of the brain of a very young specimen.  $\times 4.5$ . OB=olfactory bulb. SPS=presylvian sulcus. CQ=copora quadrigemina. U=uvula. F=flocculus. PF=parafocculus. P=pyramid.

ultimately to the olfactory tubercle. The dentate gyrus is delimited from the pallium by the *Hippocampal fissure* which runs a crescentic course bounding the periphery of the gyrus from the precommissural area to near the temporal pole of the hemisphere, where, as a surface sculpturing, it gradually becomes increasingly inconspicuous. Within the concavity of the arc formed by the dentate gyrus the *Fimbria* courses from the dorsal commissure and the olfactory peduncle above to the olfactory tubercle below. This fibre tract, although conspicuous and very distinctly marked out on the medial surface of the hemisphere, is by no means of such great relative size as it is in *Sarcophilus* or even in *Dasyurus*. The commissural connections of the two hemispheres are of paramount importance in this marsupial (see fig. 96.) The *ventral commissure* consists of a rounded bundle of

fibres lying immediately behind the precommissural area and incorporated in the septum terminale. In form and connections it is typical of the primitive condition found in other dasyurids.

The *dorsal commissure*, however, is of remarkable interest in that it would seem that the pallial fibres have proceeded to divorce themselves from those of the hippocampal complex so far as to have constituted the basis, at least, of a separate and anatomically isolated, corpus callosum. In *Sarcophilus* and other carnivorous marsupials the form of the dorsal commissure may be likened to a comma in which the relatively few pallial fibres are intermingled with those of the hippocampal complex and constitute no more of the undifferentiated commissure than the tail or dorsal and caudally directed part of the comma. In *Dasycercus*, however, these pallial "psalterial fibres" appear to be of sufficient bulk and importance to dominate the situation to the extent of demanding partial or almost total exclusion from the general dorsal hippocampal commissural bundle (see fig. 96).

Fig. 96.



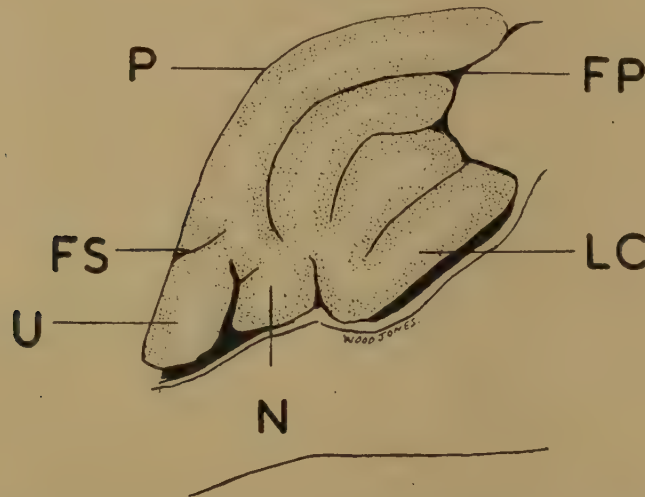
Medial aspect of the left hemisphere of the brain of a young specimen.  $\times 6$ . OB=olfactory bulb. CD=dorsal commissure. OTU=olfactory tubercle. CV=ventral commissure. F=fimbria. FD="fascia dentata". ST=septum terminale. HF=hippocampal fissure.

The degree of emancipation of the pallial fibres from those of the rhinencephalon evidently varies somewhat in different individuals of *Dasycercus*, but in no specimen was there a completely unbroken comma-shaped commissure such as is present in all the other members of the Dasyuridae that have hitherto been described. The specimen illustrated in fig. 96 was an immature animal and is typical of the well differentiated type of dorsal commissure, and it must be admitted that so far as pallial commissural development is concerned, there is but little to choose between *Dasycercus* and a macrosomic Eutherian (Monodelphian) mammal. Indeed, if comparison be made between the brain of *Dasycercus*, as a primitive insectivorous marsupial, and that of any of the small Monodelphian Insectivora, it is obvious that in relative pallial development the primitive marsupial is far in advance of the eutherian and that the possession of a corpus callosum becomes, not an absolute criterion but a matter dependent more on terminology than on the actual anatomical existence of pallial commissural fibres.



On the base of the brain (fig. 94) the *optic tract and chiasma* lie immediately behind the olfactory tubercles, from which the tracts are separated laterally by the *gyrus intermedius*. Behind the chiasma the *tuber cinereum* produces a prominent mid-line swelling, culminating in the *infundibulum*. The remarkably narrow and inconspicuous *pons varolii* lies immediately behind the tuber cinereum and the emerging nerve roots of the third, fourth, fifth and sixth nerves occupy the topographical relations typical of primitive members of the *Didelphia* and *Monodelphia* alike. Behind the inconspicuous pons the enlarged *medulla*, with the well-marked surface sculpturing of the *pyramids* and *corpora trapezoidea*, is bounded laterally by the emerging eighth nerves and the overhanging floccular lobes of the cerebellum. Here again the likeness to the primitive Eutherian condition, seen in the generalized *Insectivora*, is exact. The mid brain exposed between the caudal extremities of the hemispheres on the dorsal surface of the brain is marked

Fig. 97.



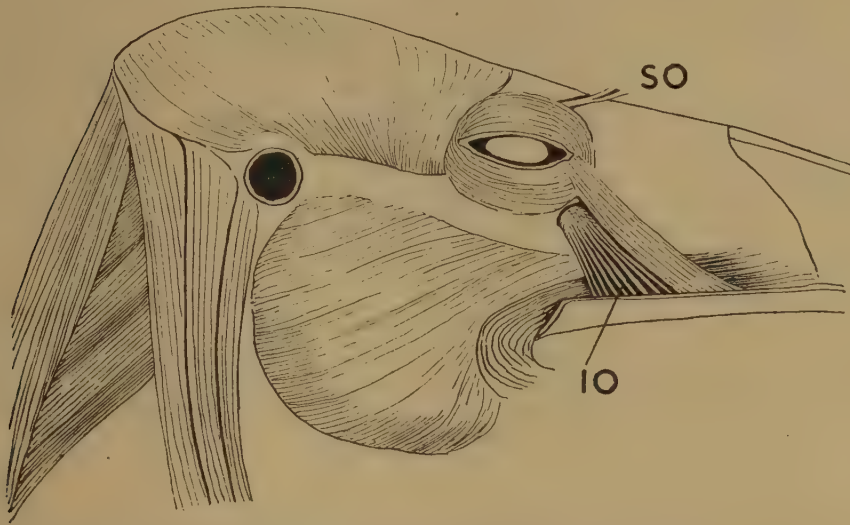
Median sagittal section of the cerebellum. FP=fissura prima. FS=fissura secunda. LC=lobus centralis. U=uvula. N=nodule. P=pyramid.

by the well-developed *corpora quadrigemina*, of which the posterior pair is the larger and more conspicuous (see fig. 95).

The *Cerebellum* is simple (see figs. 95 and 97) and it represents an extremely generalized form of the arrangement of median vermis, rounded hemispheres and prominent floccular lobes characteristic of the marsupials. The *vermis* extends forwards superficially to the posterior margin of the large *corpora quadrigemina* and so does not insert itself between the caudal extremities of the cerebral hemispheres. In this feature the cerebellum of *Dasycercus* resembles that of other primitive members of the *Dasyuridae* and so differs from that of the more specialized forms in which the vermis passes forwards on the dorsal surface of the brain to be embraced by the caudal poles of the hemispheres. The posterior extremity of the vermis terminates as the *nodule*, which rests upon the caudal portion of the roof of the fourth ventricle. The *fissura prima* is entirely concealed beneath the overhanging anterior extremity of the vermis and in this way the whole

of the anterior lobe of the cerebellum is excluded from the dorsal surface of the brain stem. The exposed portion of the cerebellum is extremely simple, consisting of a central unfoliated *pyramid* and its connecting *copula pyramidis* and *paraflocculus*. Behind the pyramid lies the *fissura secunda*, separating it from the uvula and concealed nodule. The *uvula* remains as an isolated medial elevation of the vermis, but the nodule is connected by a concealed lateral extension with the large flocculus. The sculpturing of the exposed portion of the cerebellum is extremely slight; three or four folia alone marking the subdivisions of the parafloccular lobes. The simplicity of the cerebellum of *Dasycercus*

Fig. 98.



The first and second divisions of the fifth cranial nerve, emerging onto the face to supply the facial vibrissae. SO=supraorbital. IO=infraorbital nerves.

and especially the extreme preponderance of the paleocerebellar element in its composition are doubtless to be correlated with the small size of the pons varolii already noted.

The peripheral nervous system has only been noted incidentally during the routine dissection of other systems and no departure from the usual marsupial pattern has been detected. Note was however made of the coincidence of the position of the points of emergence onto the face of the branches of the fifth cranial nerve and the disposition of the sensory facial vibrissae. Fig. 98 depicts the relatively enormous size of the intra-orbital nerve passing to the muzzle region to supply the mystacial vibrissae.

#### DUCTLESS GLANDS.

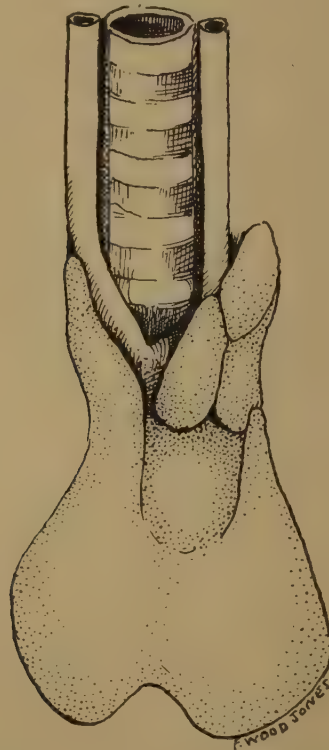
The *Thyroid* and *Parathyroid* glands are relatively small bodies situated in the neck. They lie at the sides of the laryngo-tracheal junction extending caudally to the upper rings of the trachea. They are elongated in the cranio-caudal axis and are reddish in colour. They are covered superficially by the sterno-hyoid and sterno-thyroid muscles. In form and size they are inconstant and not uncommonly



the gland mass is divided into several smaller entities extending some distance caudally at the sides of the trachea. The condition appears to be typical of the *Dasyuridae*.

The *Thymus* gland, though varying greatly in its size in different individuals, appears to persist as a functional glandular structure throughout life. The number of individuals examined is not sufficient to warrant a general statement, but in the few really adult males dissected the gland was considerably smaller than in the adult females. In immature individuals the irregularly lobed glandular mass extends over the whole of the ventral aspect of the pericardium and conceals the origin of the great vessels (see figs. 76 and 99).

Fig. 99.



The thymus gland complex in an immature female specimen.

The *Spleen* has already been described (p. 474, fig. 62) and the *Adrenal glands* are figured in connection with the kidneys (figs. 80 and 81). Of the adrenals the most striking characteristic is their wide range of variation both in position and in form. In one adult male no trace of the right adrenal was present, while the left gland was rather larger than usual and was situated on the hilum of the left kidney (this specimen has been mounted as O.100.01 in the Collection of the Royal College of Surgeons). Absence of the right adrenal has been noted by Mackenzie in the case of *Trichosurus vulpecula*.

#### PARASITES.

Although careful examination was made of both living and dead animals no ectoparasites were found on any specimen. In the peritoneal cavity of an adult



*Dasyurus cristicauda*. Adult female with seven young attached



*Dasyurus cristicauda*. Adult female from which eight young





1



*Dasyercus cristicauda*. Original figure illustrating Krefft's description. (*Proc. Zool. Soc. Lond.*, 1866, Pl. 36).

3



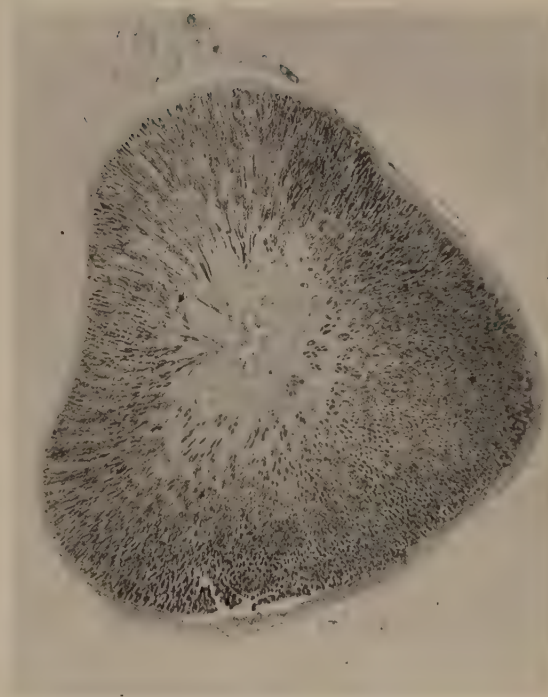
*Dasyercus cristicauda*. Rhinoglyphics of an adult male. Anterior end of rhinarium. x 16.5

2



*Dasyercus cristicauda*. Figure accompanying Baldwin Spencer's description. (*Horn Scient. Exped. to Central Australia*, 1896, Part 2. Pl. 1).

4



*Dasyercus cristicauda*. Section through the prostatic urethra of an adult male. x 25.





male about a dozen worms were present in the neighbourhood of the upper pole of the left kidney and about half that number were in the cavity of the stomach. These were submitted to Professor J. J. C. Buckley who reported them to be members of the genus *Physaloptera* too immature to permit of specific determination.

#### BIBLIOGRAPHY.

Abbreviated bibliography containing only those essential references directly related to the anatomy of the Australian Polyprotodontia didactyla.

- BEDDARD, F. E. (1908). The anatomy of *Antechinomys* and some other Marsupials. *Proc. zool. Soc. Lond.*, 1908, 561.
- CARLSSON, A. (1926). The anatomy of *Dasyuroides*. *Acta Zool., Stockh.*, 7, 249-275.
- CUNNINGHAM, D. J. (1878). Intrinsic muscles of the hand of the Thylacine, Cuscus and Phascogale. *J. Anat. Phys.*, 12, 435.
- CUNNINGHAM, D. J. (1878). The nerves of the forelimb of the Thylacine and Cuscus. *Ibid.*, p. 425.
- CUNNINGHAM, D. J. (1881). The nerves of the hind limb of the Thylacine and Cuscus. *J. Anat. Phys.*, 15, 265.
- FORDHAM, M. G. C. (1928). The anatomy of the urogenital organs of the male *Myrmecobius*. *J. Morph. Phys.*, 46, 563.
- HILL, J. P. (1900). On the female urogenital organs of *Myrmecobius fasciatus*. *Proc. Linn. Soc. N.S.W.*, 1900, 519.
- MACCORMICK, A. (1886-7). The myology of the limbs of *Dasyurus*. *J. Anat. Phys.*, 21, 103 and 199.
- MACKENZIE, W. C. and OWEN, W. J. (1919). *The glandular system in Monotremes and Marsupials*. Melbourne, p. 65.
- PEARSON, J. (1944). The female urogenital system of the Marsupialia. *Pap. Proc. roy. Soc. Tasm.*, 1944, 74.
- THOMPSON, P. (1905). Myology of the hind limbs of *Notoryctes*. *J. Anat. Phys.*, 39, 308.











*Development of the Monotremata.*—PART VII. *The Development and Structure of the Egg-Tooth and the Caruncle in the Monotremes and on the Occurrence of Vestiges of the Egg-tooth and Caruncle in Marsupials.* By J. P. HILL, F.R.S., Emeritus Professor of Embryology, and G. R. DE BEER, F.R.S., Professor of Embryology, University College, London.

(PLATES I–X.)

[Received December 9th, 1948.]

CONTENTS.		Page
INTRODUCTION .....		503
A. THE EGG-TOOTH AND CARUNCLE OF THE MONOTREMATA .....		505
List of Material. ....		505
Description of Stages I–VI. ....		505
B. EGG-TOOTH AND CARUNCULAR VESTIGES IN THE MARSUPIALIA .....		523
C. CONCLUDING REMARKS .....		526
1. Development of the Monotreme Egg-Tooth .....		526
2. Morphology of the Egg-Tooth .....		527
3. Egg-Tooth of the Squamata .....		529
4. Egg-Tooth and Caruncle: Occurrence and Function .....		531
5. The Caruncle in Monotremata and Sauropsida .....		534
BIBLIOGRAPHY .....		537
EXPLANATION OF PLATES I–X .....		540

#### INTRODUCTION.

The egg-tooth in the Monotreme was first figured by Semon (1894). In his figures 44 and 45, Taf. X. illustrating embryos of *Echidna*, approximately 9 and 11.25 mm. in G. L. respectively, the egg-tooth appears as a small conical projection, arising close behind the anterior margin of the upper jaw, precisely in the middle line and projecting downwards to overlap slightly the anterior margin of the lower jaw. But, although clearly shown in the illustrations, nowhere in the text is any reference made to an egg-tooth. This oversight, however, was made good by Seydel (1899) who gave an account of the development and structure of the egg-tooth in *Echidna* based on the examination of five embryos in Semon's collection (embryos 43–46, ranging in G. L. from 6.5 mm. to 14.5 mm.). In his youngest stage (embryo 43) he describes the egg-tooth, viewed in section, as having the same form as that seen in Semon's figure 44 and as consisting of a downwardly projecting cone-shaped mass of compactly arranged mesodermal cells, clothed externally by a layer of epidermis, continuous with that investing the rest of the head. In embryo 44 (Semon's figure 44), the freely projecting tooth has attained a length of 0.25 mm. and exhibits a distinct advance on that of embryo 43, inasmuch as there is now present between the mesoderm (the future pulp) and the enclosing epidermis, a thin, cone-shaped layer of "Hartschubstanz", perfectly homogeneous, which the author regards as dentine or at least as related to dentine. At its base, this layer is directly connected by fine bone-trabeculae



(similar in character to the dentine) with the trabecular network of the developing premaxillae. Furthermore, the cells of the pulp, adjoining the dentine have now assumed a low columnar or cubical form and have taken on an epithelial-like arrangement. They are stated to resemble in appearance the osteoblasts of the bone-trabeculae and to form a layer of odontoblasts, probably concerned in the formation of the dentine. In this embryo the epidermal covering of the tooth had largely been lost.

In the next stage (embryos 45 and 45\*) the tooth measures in length 0.21 mm. The dentinal cone has thickened and terminates in a pointed apex. In the epidermal layer investing the tooth, the basal cells are described as cubical or columnar in form and as abutting directly on the surface of the dentinal layer. Though the author fails to recognize these cells as ameloblasts and is unable to detect a layer of enamel in the sections, he thinks it probable that a thin layer is present judging from the glossy appearance of the tooth of embryo 46 when examined intact in alcohol. The pulp tissue has now loosened and is penetrated by capillaries, whilst the connective tissue elements in it have become more numerous.

In the last stage described (embryo 46, shortly before hatching), the tooth is stated to have attained its maximum development. Indeed it already shows signs of retrogression. Its epidermal covering has disappeared; degenerative changes are evident in the pulp and osteoclasts are now present in relation to the bone-trabeculae connecting the dentinal shell with the premaxillae. In the pouch-young of 20 mm. G.L., represented in Semon's figure 47, Taf. XI, Seydel states that the egg-tooth has completely disappeared.

Green (1930) provided for the first time an account of the structure of the egg-tooth in *Ornithorhynchus*, based on the study of sections of a recently hatched nestling with a G. L. of 16.5 mm. (specimen "W", twin of "WW", described in the present communication). His description shows that the egg-tooth of *Ornithorhynchus* differs in no essential way structurally from that of *Echidna*, and that as in the latter, the base of its dentinal shell is firmly connected by bone-trabeculae with the premaxillae so that the tooth is remarkably well supported.

Seydel and Green both called attention to the similarity in the mode of development of the Monotreme egg-tooth and the transitory toothlets first described by Röse (1893) in the Crocodile, whilst Seydel expressed the view that the egg-tooth of *Echidna* is the remnant of an old tooth-generation, long ago suppressed.

Our own observations, based on a more adequate material than was available to these two investigators, whilst largely confirming and considerably extending their results, have established a new fact of some little interest, and that is the presence in the developing egg-tooth of the Monotreme of a well-developed enamel organ, possessing the normal constituents of such an organ (ameloblastic layer, stellate reticulum and outer layer) which is differentiated, not from a dental lamina, but directly from the epidermis investing the mesodermal (dentinal) papilla of the tooth, a mode of development the Monotreme egg-tooth shares with the transitory toothlets of the Crocodile as Seydel and Green recognized.

The fact that the Monotremes are unique among the Amniota in the possession of both an egg-tooth and a caruncle does not appear to have been emphasised by

any previous investigator. We are able to add new details concerning the latter structure and its supporting bony nodule, the os carunculæ.

We are also able to provide an account of the occurrence of vestiges of the egg-tooth and the caruncle in the Marsupialia.

One of us (H.) desires to express his grateful thanks to the Wellcome Trustees for a grant. We are much indebted to Mr. F. J. Pittock, F.R.P.S., A.L.S., for the skill and care he has expended on the preparation of the photo-micrographs, and to Mr. H. Barker for his efficient technical assistance.

#### A. THE EGG-TOOTH AND CARUNCLE OF THE MONOTREMATA. MATERIAL.

The monotreme material at our disposal comprises eight embryos of *Platypus* from the laid-egg, one embryo of *Echidna* from the pouch-egg, just prior to hatching, and one early nestling of *Platypus*, a total of ten specimens. These we have grouped into six stages as follows:—

Stage 1. Twin embryos of *Platypus*, KK., G.L. 8 mm. Trans. Series.

K., G.L. 8.5 mm. Long. Series.

Stage 2. *Platypus* L., G.L. 9 mm. Trans. Series.

Stage 3. Twin embryos of *Platypus*, V., G.L. 8.5 mm. Trans. Series.

VV., G.L. 8.5 mm. Trans. Series.

Appendix to Stage 3. GW.1, G.L. 9 mm., just earlier than V. Trans. Series.

G.W. 2, G.L. 9 mm., very similar to VV. Trans. Series.

Stage 4. GW. 3, G.L. 10 mm. (?+) Trans. Series.

Stage 5. *Echidna* EBB., G.L. 12.5 mm., H.L. 6.75 mm. Trans. Series.

Stage 6. *Platypus* WW., G.L. 16.75 mm., H.L. 6 mm. Trans. Series.

#### DESCRIPTION OF MATERIAL.

##### *Stage I.*

Twin embryos. *Platypus* K., G.L. 8.5 mm. Long. Series.

KK., G.L. 8.0 mm. Trans. Series.

Intermediate between Semon's *Echidna* embryos 43 and 44.

Pl. I, figs. 1-4.

In median sagittal section (Pl. I, fig. 1) the egg-tooth primordium is seen to be already well established as a median projection of triangular outline, which arises by a broad base from the under-side of the protuberent snout region of the head, directly below the caruncular eminence, and projects downwards and slightly backwards, beak-like, gradually narrowing to its bluntly pointed apex. It all but occludes the median part of the oral opening and overhangs the bevelled anterior margin of the lower jaw primordium. Its longer, slightly curved cranial surface practically follows the contour of the cranial surface of the head, being interrupted only by a slight indentation marking its base, whilst its shorter almost straight caudal surface joins the roof of the buccal cavity practically at a right angle.

The tooth-primordium projects beyond the general surface-level for a length of approximately 0.20 mm. in KK and 0.23 mm. in K. Its cranio-caudal thickness at its base measures 0.30 mm. in KK and 0.272 mm. in K, whilst its transverse width at its base in KK is 0.28 mm.



It has the form accordingly of a freely projecting cone, slightly curved backwards and, as the measurements show, slightly laterally compressed. It has evidently been formed by a localized papilliform downgrowth of the mesenchyme of the head, which, indenting the underlying epidermis, has carried the latter with it in its growth, to form its external epidermal covering.

Surrounding the base of the projecting portion of the primordium is a shallow surface-groove, the basal groove, which is distinct round its lateral and caudal surfaces (Pl. I, figs. 3 and 2, *b.gr.*) but on its cranial surface appears only as a slight indentation. It marks the site of an infolding of the epidermis, the basal fold as we may term it, which projects rim-like into the mesenchyme, being more prominent round the cranial and lateral sides of the primordium than it is caudally (Pl. I, figs. 2 and 3, *b.fd.*). Its inner or deep margin marks the base of the tooth, whilst the fold itself is destined to form the basal portion of the enamel organ.

Laterally to the tooth, the epidermal layer (Pl. I, figs. 3 and 4, *b.ep.*) (now established as such all over the head) is thicker adjacent to the basal groove than it is more peripherally and consists of (*a*) a basal layer of low columnar or cubical cells, resting on a very thin basement membrane; (*b*) an intermediate zone, in continuity with the basal layer, composed of two or three superimposed layers of more or less rounded cells, fairly compactly arranged; and (*c*) a thin superficial layer formed of flattened nucleated cells, one cell thick. On approaching the basal groove, the epidermis dips inwards to form the basal fold above-mentioned, and, at the same time, its basal layer gradually thickens, reaching its maximum over the groove, as the result of the assumption by its cells of a high columnar form, whilst the cells of the intermediate zone lose their compact arrangement. In the interior of the fold where they have increased in number, they become more or less widely dispersed and separated by large intercellular spaces. They remain, however, connected with each other and with the superficial layer by delicate cytoplasmic processes, and so form a very irregular network, which we may regard as the first trace of the stellate reticulum of the future enamel organ (Pl. I, fig. 4).

On the medial side of the basal groove, the epidermis of the basal fold continues onward to form the outer investment of the mesodermal core constituting the dentinal papilla or future pulp of the tooth. It has already undergone significant alterations. Its basal layer (Pl. I, fig. 4, *e.ep.*) is now in process of taking on the form of a columnar epithelium and has largely lost connection with the cells of the intermediate zone, with the result that it is acquiring a continuous contour on its outer surface. Its inner surface rests on a basement membrane, which is rather thicker than that of the epidermis immediately surrounding the tooth. This layer we can identify as the enamel epithelium or layer of ameloblasts of the future enamel organ. It reaches a thickness of 0.013–0.015 mm. and is composed of low columnar cells with oval nuclei, situated centrally or towards the outer ends of the cells. Intermingled with the normal cells there occur in small numbers and mostly singly, slender deeply staining cells with small flattened nuclei, of unknown significance but possibly degenerate.

Outside the enamel epithelium, the cells of the intermediate zone have begun to loosen apart, especially in the region adjacent to the basal groove in embryo KK,

but over most of the tooth in K and over its apex in KK, they still retain their compact arrangement.

The mesodermal core (dental papilla) of the tooth (Pl. I, fig. 2, *d.p.*) is composed of a mass of compactly arranged mesenchyme cells and into it capillaries have already penetrated. But already, starting from the level of the inner margin of the basal fold and extending all over the surface extent of the papilla, it can be seen that its superficial cells have enlarged and are assuming a cubical or narrow columnar form, and a disposition more or less at right angles to the basement membrane of the enamel epithelium. In the basal region of the papilla especially, there are indications that they are taking on an epithelial-like arrangement (Pl. I, fig. 4, *od.*). These cells are destined to form the layer of odontoblasts which clothes the surface of the papilla in later embryos.

The massive rounded elevation, seen in sagittal section in Pl. I, fig. 1, *car.*, projecting from the dorsal aspect of the head and bounded behind by a deep groove constitutes the caruncle. It is formed by a large projecting mass of mesenchyme, covered by epidermis which is not yet specially thickened. In the mesenchyme of the caruncle and located mainly in its cranial half, is a fairly definitely localized area of condensation (indicated by its deeper staining) (Pl. I, fig. 1, *c.os.c.*) which can be followed, on the one hand, obliquely backwards and downwards into continuity with the large condensation on the left in the figure, representing the primordium of the nasal septum (*n.s.c.*) and on the other, almost directly downwards into the band-like "rostral" condensation which runs down shortly below and practically parallel with the frontal epidermis (*m.d.c.*). The caruncular condensation probably constitutes the site of formation of the os carunculæ and the band-like condensation that of the ascending processes of the premaxillæ.

#### Stage II.

Platypus embryo, L., G.L. 9 mm.

Pl. I, fig. 5 and Pl. II, fig. 6.

The egg-tooth (Pl. I, fig. 5, Pl. II, fig. 6) is slightly longer and its apex is rather more pointed than that of KK. It is difficult to measure the length of the tooth accurately but if we take the extent of its projection beyond the general surface-level, we obtain an approximate measurement of its length in the various embryos. That measurement in this embryo gives the tooth a length of 0.26 mm. as compared with 0.20 mm. in KK and 0.23 mm. in K. The distance from the tooth-apex to the inner margin of the basal fold can be measured more accurately and that yields a length of 0.35 mm. in this embryo as compared with 0.28 mm. in KK; from which we may conclude that the dental papilla has increased slightly in length and has also increased in thickness as measured at the level of the basal fold, its thickness here being 0.12 mm. as compared with 0.098 mm. in K.

The enamel organ (Pl. II, fig. 6,) has made progress in differentiation and now can definitely be recognized as such. The enamel epithelium (*e.ep.*) though no thicker than in KK (about 0.013 mm.), is a quite well-defined layer, with a continuous limiting membrane on its outer surface and with its inner surface resting on the basement membrane (*b.m.*). It is composed of low columnar cells, with large oval nuclei, situated more or less centrally and tending to alternate



with each other. The stellate reticulum (*s.r.*) is now differentiated over the extent of the enamel organ, with the exception of its apex. Immediately outside the enamel epithelium, however, the cells tend to form a more compact layer, recalling the stratum intermedium in the enamel organ of higher Mammals. The external enamel epithelium (*o.ep.*) is distinct as a thin layer of flattened cells.

It is worthy of note that the intercellular spaces seen in KK between the stellate cells occupying the basal fold have now coalesced to form a practically continuous ring-shaped space or canal, situated in the base of the enamel organ (Pl. II, fig. 6, *b.sp.*). In this figure, on the left, a small capillary (*cap.*) overlies the basal layer of the epidermis of the basal fold, which roofs over the just mentioned canal, and it is noteworthy that this roofing portion of the basal layer already shows signs of thinning.

The basement membrane (Pl. II, fig. 6, *b.m.*) on which the enamel epithelium rests, is now distinctly thicker than in KK, its thickness being about 0.001 mm. It appears perfectly homogeneous and, being strongly eosinophil, stands out prominently in the sections.

The dentinal papilla, apart from a distinct increase in its vascularity, shows no marked advance on that of KK. Its odontoblastic layer (Pl. II, fig. 6, *od.*) however, has made some progress, though it is not yet clearly marked off from the cell-mass of the papilla and appears somewhat irregular in character. The odontoblasts vary considerably in form and size, from cubical cells (0.013 mm. in height), to columnar (0.019 mm.) and narrow club-shaped cells (up to 0.021 mm.). Their nuclei are oval or rounded, relatively large and basally situated. The cells are separated from each other by fine clefts, and frequently their flattened apical ends appear to be separated from the basement membrane by fine clear gaps.

The section shown in Pl. I, fig. 5 passes through the egg-tooth and the caruncle shortly in front of the narial openings. In the mesenchyme directly above the egg-tooth is a median mesenchymal condensation, distinguishable into a rather lighter median strip and darker lateral wings. These latter form the sites of formation of the medial laminae of the premaxillae, and already there are present, between the cells, traces of extremely fine eosinophil fibrillae which herald their commencing formation (*m.px.p.*). That the premaxillae should be the first of the bony elements of the skull to make their appearance is a fact of some little interest, bearing witness as it does to the importance of the caruncle in the economy of the Monotreme embryo, the ascending processes of the premaxillae acting as struts for the support of the os carunculae.

In Pl. I, fig. 5 it can be seen that the median condensation in question is continued dorsally as a septal-like prolongation (*md.c.*) between the arc-shaped condensations for the marginal cartilages of the snout (*m.c.*), which terminates above in the caruncular condensation (*c.os.c.*).

### Stage III.

Platypus V and VV. G.L. 8.5 mm.

In egg-tooth development, V is well in advance of L and VV is slightly more advanced than V.

The nasal capsule is in the procartilaginous stage, and the dentinal layer and bone-trabeculae have appeared.

*Embryo V.* (Pl. II, figs. 7 and 8.)

The measurements of the egg-tooth indicate a slight increase over those of L. Its projection beyond the general surface-level measures 0.29 mm. as compared with 0.26 mm. in L, whilst the length from the tooth-apex to the inner margin of the basal fold is now 0.39 mm. as compared with 0.35 mm. in L. The thickness of the dentinal papilla at the level of the basal fold also shows an increase from 0.12 mm. in L. to 0.17 mm.

The enamel organ (Pl. II, fig. 7) shows no very noteworthy advance on that of L. The stratum intermedium, indicated in L, is rather more distinct, whilst the basal ring-shaped space (*b.sp.*) has increased somewhat in size and the basal layer of the epidermis forming its roof shows further evidence of thinning, small capillaries lying in direct contact with it (Pl. II, fig. 8, *cap.*). The enamel epithelium is essentially similar to that of L.

The basement membrane is now represented by a deeply staining refractive layer, with a rather wavy contour and a thickness of about 0.002 mm. This layer we regard as dentine (Pl. II, figs. 7 and 8, *den.*). It lies in intimate contact with the under-surface of the enamel epithelium, but over much of its extent it is separated by a contraction-space from the odontoblast layer and, so far as we have been able to observe, no dentinal fibres penetrate into it. The dentinal layer can be traced over the basal fold into continuity with the basement membrane of the surrounding epidermis (see Pl. III, fig. 12 of VV); we can thus conclude with certainty that its basis is furnished by that membrane. In a few sections, we have observed a nucleus included in it and occasional flattened cells are to be found closely applied to its deep surface, but the occurrence of such included nuclei, and detached cells is exceptional.

The dentinal papilla has undergone a striking change and has lost its former uniformity. It is now permeated by a plexus of capillaries (derived from branches of the two large paramedian (rostral) vessels seen in the upper half of fig. 7, *r.v.* Pl. II), the meshes of which are occupied by clumps of enlarged mesenchyme cells. The papilla is thus in process of acquiring the characters of a genuine pulp.

Concomitantly with this change, the odontoblasts (Pl. II, fig. 8, *od.*) have come to form a distinct, easily recognizable layer, though it is still somewhat irregular in character owing to variation in the form and size of the cells. They are mostly cubical or low columnar in form, with large, basally situated oval or rounded nuclei, and range in height from 0.015–0.017 mm.

One other advance (already faintly indicated in L) is seen in the appearance in the mesenchyme of two paired groups of bone-trabeculae, constituting respectively the primordia of the medial laminae of the premaxillae and the attaching bone of the egg-tooth, which arise quite independently of each other.

The attaching bone-primordia (Pl. II, figs. 7 and 8, *at.b.*) are the better developed of the two. They take the form of fine strands or trabeculae, irregularly branched and connected together, net-like, which lie above and medially to the basal fold. They stain similarly to the dentine and may be traced between the odontoblasts



into direct continuity with it (Pl. II, fig. 8). The odontoblasts moreover, pass directly into the dense mass of enlarged cells between which the trabeculae are situated and which form actual or potential osteoblasts. The trabeculae extend up towards the premaxillary primordia and here and there become continuous with them.

The paired premaxillary primordia (Pl. II, figs. 7 and 8 *m.px.*) are situated in the mesenchymal condensation occupying the space between the two large "rostral" vessels (*r.v.*) seen shortly above the egg-tooth in the figures and take the form of two vertically running strands, very delicate and slightly branched, which lie one on either side of the middle line, just medial to the mentioned vessels. Other strands disposed more or less horizontally, immediately above the base of the dentinal pulp, form an incomplete connection between their lower ends.

It may be mentioned here that the two vessels which for descriptive purposes we have termed "rostral", pass outwards, caudally to the termination of the dentinal pulp, to a more lateral position and finally largely lose their identity in the capillary plexuses in the upper jaw mesenchyme.

#### *Embryo VV.*

Pl. II, fig. 9, Pl. III, figs. 10-13, Pl. IV, fig. 14.

In its dimensions, the egg-tooth of VV closely agrees with that of V, but its projection beyond the surface-level is slightly greater, 0.32 mm. as compared with 0.29 mm. in the latter. In degree of development of bone trabeculae, VV is, however, distinctly in advance of V, and the same holds true for the enamel organ which is nearing the height of its development (Pl. II, fig. 9; Pl. III, figs. 10 and 13). In the figures, the external enamel epithelium (Pl. III, fig. 10, *o.ep.*) is evident as a layer of flattened cells, continuous with the superficial layer of the epidermis. The stellate reticulum (Pl. III, fig. 13, *s.r.*), now a conspicuous layer, quite well developed, is composed of spindle-shaped cells, giving off fine anastomosing processes. It extends between, and is continuous with the external epithelium on the outside and a compact layer of cells, one to two cells thick, the stratum intermedium (Pl. III, fig. 12, *st.i.*), on the inside, covering the outer surface of the enamel epithelium. Over the tip of the tooth, the stellate reticulum is not yet differentiated. The basal ring-shaped space (Pl. III, figs. 10 and 12, *b.sp.*), crossed here and there by spindle-shaped cells, has notably enlarged, and the dorso-lateral portion of its roof, formed practically only by the basal layer of the epidermis and overlain as in earlier embryos by capillaries (Pl. III, fig. 12, *cap.*), has in places become reduced to a quite thin layer. We suggest that this space is of the nature of a lymph-space which provides for the supply of nutrient materials to the cells of the enamel organ and which is rendered necessary by the freely exposed position of the latter and its entire lack of a blood-supply. The enamel epithelium (Pl. III, fig. 13, *e.ep.*), a little thicker on the average than that of V, shows no essential difference from that.

The dentinal pulp (Pl. III, fig. 12, *d.p.*) is also very similar to that of V, as is the layer of odontoblasts, well seen in figs. 12 and 13 (*od.*) (Pl. III). The "dentine" (*den.*) has increased in thickness to about 0.003 mm., presents a slightly

wavy contour and stains deeply and uniformly. Between it and the flat surfaces of the odontoblasts is a thin layer of a lighter staining, faintly granular material probably in continuity with it and representing uncalcified "pre-dentine". That the odontoblasts are the chief agents concerned in the formation of the "dentine" is shown by the sudden decrease in its thickness coincident with the cessation of the odontoblastic layer at the level of the inner margin of the basal fold. Here the dentinal layer becomes directly continuous with the basement membrane of the epidermis (Pl. III, fig. 12, *b.m.*).

Behind the caudal limit of the enamel organ as a distinct surface-projection, the root of the tooth continues onward for a distance of 0.05 mm. before the odontoblasts, dentine and pulp finally disappear.

The premaxillary and attaching bone-trabeculae in this embryo reach a distinctly higher degree of development than in V but are still very slender. The premaxillary primordia are a little more extensive than the egg-tooth. They first appear in the serial sections over the anterior margin of the tooth and end about 0.07 mm. behind the termination of the dentinal pulp. At their caudal extremity, they appear as two thin slightly branched trabeculae, paramedian and disposed vertically. They lie medially to the two rostral vessels which are acquiring their definitive paramedial position. Traced forwards in the sections (Pl. III, fig. 11, *m.px.*) they are seen to become connected at their lower ends by a delicate cross-piece. At the same time, delicate trabeculae (*l.px.*) have appeared below and laterally to the rostral vessels, in continuity with the paramedian primordia. Subsequent stages show that these laterally situated trabeculae are the primordia of the lateral laminae of the premaxillae, whilst the first-mentioned paramedian trabeculae are the primordia of their medial laminae. The attaching bone-trabeculae as we have seen in V, appear coincidently with the dentinal layer of the tooth and in continuity with it. They extend upwards on each side to become continuous with the lateral premaxillary trabeculae and the lateral extremity of the cross-piece between the paramedian trabeculae which has extended outwards. In Pl. III, fig. 11, this cross-piece is seen to form a conspicuous but thin arc-shaped band, arching over the dentinal pulp and in continuity at its outer ends with the attaching bone-trabeculae. Later stages show that it really forms part of the latter system. It becomes interrupted, in front, by the downward passage on each side, of a large branch of the "rostral" vessel to the capillary plexus of the dentinal pulp. At the same time, the two "rostral" vessels meet and anastomose dorsally to the medial premaxillary primordia (Pl. III, fig. 11, *r.v.*) and from the anastomosis a median caruncular vessel passes up to the capillary plexus in the caruncular mesenchyme. At this level, the lateral premaxillary primordia are no longer present, whilst the medial have increased in size, attaining their maximum immediately cranial to the caruncular vessel. They now begin to extend dorsally in the median "rostral" condensation which runs upwards from above the egg-tooth, as two distinct, vertically disposed trabecular processes which we can identify as the primordia of the ascending (prenasal) processes of the premaxillae (Pl. III, fig. 10, *a.px.*). Over the lower half of their extent, they appear as two elongated narrow bands, with somewhat irregular contours, composed of fine trabeculae and situated on either side of a dense cellular tract which runs up



in the median line between them (Pl. II, fig. 9, and Pl. III, fig. 10, *md.c.*). After a course of about 0.20 mm., they rapidly become reduced to a few fine eosinophil fibrils which can be traced up to within a short distance of the apparent termination of the above-mentioned median tract (Pl. IV, fig. 14, *a.px.t.*). This latter is merely the median portion of the main septal condensation which extends upwards from above the egg-tooth to the base of the caruncle, passing through the gap between the developing marginal cartilages of the snout (Pl. II, fig. 9, *m.c.*), and in whose wings the trabeculae of the ascending processes arise. It terminates above in a rather poorly defined but definitely recognizable median mass of cells situated in the base of the caruncle (Pl. II, figs. 9 and 14, *c.os.c.*). This mass we regard as the site of formation of the os carunculae. In it, distinct traces of eosinophil fibrils and matrix material can already be detected between the cells, and we would emphasize, they have been formed entirely independently of those of the ascending processes of the premaxillae. We are, accordingly, led to the conclusion that the os carunculae does not arise by the fusion of the upper ends of these processes as previous writers (Wilson (1902), Green (1930), de Beer and Fell (1936)) have assumed. Rather must this unique bone be regarded as an independent ossification with which these processes later unite.

In this embryo, the epidermis clothing the caruncular projection (Pl. IV, fig. 9, *car.*) is slightly thickened over its apex and consists of a basal layer, three or four strata of nucleated cells, and traces of a thin layer of flattened cells at the surface. On one side of the apex, however, the superficial layer is distinct and appears to have undergone some cornification.

#### *Appendix to Stage III.*

##### *Platypus GW. 1.*

G.L. (approx.) 9 mm. Just earlier than Platypus V.

Pl. IV, fig. 15.

The egg-tooth agrees fairly closely with that of V in its dimensions, but is a shade longer, 0.32 mm. as compared with 0.29 mm. in V. Its enamel organ (Pl. IV, fig. 15), however, approximates more to that of VV in the condition of its stratum intermedium and stellate reticulum. Owing to contraction, the enamel epithelium (*e.ep.*) is separated by a space containing some detritus material from the dentinal layer. It is well developed and about 0.014 mm. in thickness.

The pulp is richly vascularized by large capillaries and the odontoblast layer is clearly differentiated and well marked off from it (Pl. IV, fig. 15, *od.*). The dentinal layer (*den.*) appears as a wavy membrane, with a fairly uniform thickness of about 0.003 mm. It has stained lightly and is possibly not yet fully calcified, but on its outer surface, next the enamel epithelium, there is present a very thin layer, which has stained deeply, the significance of which is not clear. It may be the first trace of enamel.

No bone-trabeculae have as yet been formed, but aggregates of osteoblasts in the sites of the attaching bone and premaxillae are clearly recognisable (Pl. IV, fig. 15, *ost.*) and caudally, in the region of the root of the tooth, traces of the matrix of the attaching bone can be seen between the osteoblasts.

*Platypus* GW.2.

G.L. 9 mm. This embryo approximates closely to VV.

Pl. IV, fig. 16.

The egg-tooth is of the same length as that of V. viz. 0.29 mm., whilst its enamel organ is very similar to that of VV. The basal space is large and the stellate reticulum well developed except over the apex of the tooth (Pl. IV, fig. 16, *b.sp.*). The enamel epithelium (*e.ep.*) is thin, 0.01 mm., but otherwise is normally developed. As in GW. 1, a contraction-space separates it from contact with the dentine.

The pulp is richly vascularized as in GW. 1 and even more so than in that of VV. The odontoblast layer, very distinct in the sections (Pl. IV, fig. 16, *od.*) varies in thickness from 0.013 to 0.017 mm. and is very similar to that of VV. The odontoblasts are mostly plump columnar cells of slightly varying height, with homogeneous dark staining-cytoplasm and basally situated oval or round nuclei, each with an eosinophil nucleolus. Above the basal fold, they pass over into the aggregations of osteoblasts in which the trabecular matrix of the attaching bone is being laid down.

The dentine owing to fixation-contraction has the same wavy contour as in GW. 1. It is slightly thicker than in the latter, measuring 0.004 mm., is distinctly refractive and stains fairly deeply, from which we conclude that it is well calcified. There are indications of the presence on its outer surface of the same deeply staining film-like layer which we encountered in GW. 1.

The primordia of the medial laminae of the premaxillae and the attaching bone agree very closely in their degree of development with those of VV, but the ascending processes of the premaxillae are less extensive than in the latter and appear to terminate well below the base of the caruncular condensation.

*Stage IV.**Platypus*, GW. 3.

G.L. stated to be "10 mm." Developmentally this embryo is distinctly in advance of VV and in external form closely agrees with Semon's stage 45 of *Echidna* with a G.L. of about 11.25 mm.

Pl. IV, fig. 17, Pl. V, figs. 18-22.

The egg-tooth, in its dimensions, agrees closely with that of VV. In particular, it is precisely of the same length (0.32 mm.), so that in the interval, there has been no growth in length. In other respects, however, notably in bone-development, this embryo is in advance of VV.

The enamel organ (Pl. IV, fig. 17) has practically reached its maximum development. The stellate tissue consists of very slender spindle-shaped cells, slightly branched, which run obliquely from the now reduced stratum intermedium to the external layer, and now extend continuously over the apical part of the tooth. The basal space (*bs.p.*) is still present but is smaller than in preceding stages and the capillaries overlying its thin roof formed by the basal layer of the epidermis, appear reduced. The enamel epithelium, with a maximum thickness of about 0.010 mm. is thinner than in VV and the odontoblast layer also appears less well developed, but its preservation is not quite perfect. The dentine (Pl. IV, fig. 17, *den.*) on the other hand, is thicker than that of VV, reaching a thickness



of 0.0043 mm. as compared with 0.003 mm. in the latter. In the section illustrated, it appears as a deeply stained, perfectly homogeneous layer, with below it, a thin unstained layer of uncalcified pre-dentine. In other sections, however, the dentine has stained a lighter tint and on its outer side there is present a thin layer which has stained deeply. Whether or not this represents the enamel must remain uncertain.

The dentinal pulp now presents the appearance of a loose connective tissue and is still very vascular (Pl. IV, fig. 17, *cap.*). As in preceding stages, it projects well above the basal fold.

In its bone-development, this embryo exhibits striking progress. The trabecular networks of attaching bone have increased greatly in extent and have become calcified and much more massive, whilst the premaxillary primordia have also increased as the result of the laying down of additional matrix, but, it should be noted, calcification occurs later in them than in the attaching bone, and whilst it has set in in the medial laminae (Pl. IV, fig. 17, *m.px.*), it is not yet apparent in the lateral (*l.px.*).

In Pl. IV, fig. 17, the contrast between the deeply stained trabecular networks of attaching bone (*at.b.*) situated above the basal fold, and the lighter stained premaxillary primordia (*m.px.* and *l.px.*) lying above them, is strikingly illustrated. The latter primordia, at the level of this figure are represented by four ossific areas; two are paramedian (*m.px.*) and situated medially to the two rostral vessels (*r.v.*) and two are lateral (*l.px.*) to the same. The former are destined to form the medial laminae of the premaxillae and the latter, their lateral laminae. It will be observed that calcification of the matrix has already commenced in the medial laminae.

At this level, the laminae, medial and lateral, do not differ greatly in size. Caudally, however, in the region of the root of the tooth, the lateral laminae become much larger than the medial and form extensive wing-like areas, extending well out into the surrounding mesenchyme (Pl. V, fig. 18, *l.px.*).

The attaching trabecular network on each side (Pl. IV, fig. 17, *at.b.*) is seen to be connected on the one hand with the dentinal shell of the tooth and, on the other, with the lateral lamina and the irregular arch of bone overlying the pulp and connecting the lower edges of the medial laminae.

Tracing the premaxillary laminae cranially from the level of Pl. IV, fig. 17, the lateral laminae are found to approach the medial and to unite with them over the anterior margin of the tooth. Beyond this, the two medial laminae, now somewhat enlarged, continue upwards, cranially to the tooth, as two well-defined, laterally compressed bands, the ascending processes of the premaxillae (Pl. V, fig. 19, *a.px.*). They remain separate over a length of 0.10 mm. and then become connected by a cross-anastomosis, giving them a dumb-bell like shape. Continuing on for 0.05 mm., they finally form a transverse band which becomes continuous with the base of the developing os carunculae (Pl. V, fig. 20, *a.px.* and *os.c.*). The ascending processes have a total length in the sections of about 0.15 mm. They consist of an eosinophil matrix containing sparse lacunae, occupied by osteocytes and are surrounded by a layer of osteoblasts.

*Caruncle and os carunculae.*

The sections of the caruncle in this embryo are obliquely transverse to its long axis. The developing os carunculae occupying its central region (Pl. V, fig. 21, *os.c.*), is now a quite well defined formation with a distinctive appearance and structure which distinguish it from the fused ascending premaxillary processes with which it is continuous at its base, as stated above (Pl. V, fig. 20).

The histogenesis of this unique membrane-bone presents some peculiar features for which we have been unable to find precise parallels in the descriptions of the development of membrane-bone in other Mammals.

At this stage of its development the bone consists of an inconspicuous lightly staining uncalcified matrix enclosing numerous lacunar spaces in which the cells (osteoblasts, osteocytes) are situated (Pl. V, figs. 21 and 22, *lac.*). The matrix (Pl. V, fig. 22, *m.*) takes the form of a fine network, the strands of which are of very variable thickness and finely fibrillar in texture, and whose meshes appear as lacunar spaces, roughly ovalish or rounded in form, which vary in size and lie irregularly crowded together. Under low power examination, these lacunae constitute the most striking feature of the developing bone at this stage, since many of them appear as clear spaces, owing to the close adherence of the cells they contain to the enclosing matrix. Such lacunae occur especially in its central region, but they are also present peripherally as well (Pl. V, fig. 21). They are lined by a few more or less flattened osteoblasts, frequently accompanied by a curious type of cell with a thin crescentic cell-body and a small oval nucleus, the whole staining deeply and uniformly. The central space in such lacunae usually appears to be empty but it may contain one or two lightly staining cells. Lacunae of this type represent one extreme; at the other are smaller lacunae, situated peripherally, especially in the upper and lower marginal regions of the bone, which are separated from each other by a very thin layer of matrix and are completely filled by a loose group of six or more cells with large oval or rounded nuclei (Pl. V, fig. 22, *ost. gr.*). These cells we can identify as osteoblasts since they appear to be identical with the osteoblasts of the osteoblastic zone which encloses the bone (Pl. V, fig. 22, *ost.*). Between these two extremes, we meet with a variety of intermediate stages, *e.g.*, lacunae in which the osteoblasts have loosened up still more and distinct spaces have appeared between them, others in which the osteoblasts form a peripheral layer surrounding a small central space, and yet others, somewhat larger, in which a discontinuous peripheral lining of osteoblasts, closely applied to the matrix, is recognizable, enclosing a central space either empty or containing one or two cells. The peripheral osteoblasts in such lacunae vary considerably in form; they may be crescentic, cuboidal or ovoidal, and included amongst them is usually to be seen a readily recognizable type of cell, referred to above, the small crescentic cell with a flattened oval nucleus which stains intensely. The significance of these small cells is not clear. They are probably degenerate and may be fibroblasts which have failed to transform into osteoblasts. No trace of them is to be found in the lacunae of the bone in *Platypus* WW.

The bone is enclosed by an osteoblastic zone, which attains its maximum thickness along its upper margin. Here the osteoblasts are more compactly



arranged than they are laterally and below, and merge into the upper region of the bone where they are becoming segregated into groups by the formation of fine strands of matrix between them. Although the bone increases in size by additions all over its circumference, its main growth-centre appears to be located along its upper margin.

Outside the osteoblastic zone is a second thicker periosteal zone, composed of smaller cells and clearly distinguishable from the surrounding mesenchyme.

The approximate dimensions of the os (exclusive of the osteoblastic zone) as measured in the sections are as follows:—Cranio-caudal length, 0.13 mm., Transverse thickness, 0.17 mm., Vertical height, 0.32 mm. (Owing to the sectional plane, these measurements, it should be noted, are not comparable with those of the os in *Platypus* WW.)

Finally we may remark that the structure of the developing os in this embryo supports the contention previously made (*ante*, p. 512) that it is to be regarded as an independent ossification.

The epidermis over the apical surface of the caruncle has a thickness of 0.043 mm. as compared with 0.025 mm. over its lateral surface. It consists of a basal layer of cubical cells, above which are five to six layers of flattened cells which become progressively more squame-like as the surface is approached. Forming the surface is what appears to be a non-cellular cuticular layer, in the form of a deeply staining thin membrane.

#### *Stage V.*

*Echidna* EBB.

G.L. 12.5 mm. H.L. 6.75 mm.

Pl. VI, figs. 23–26; Pl. VIII, figs. 27 and 28; Pl. IX, fig. 41.

This embryo of *Echidna*, the only one we have available for examination, is at the stage just prior to hatching. When removed from the shell, it was found to be devoid of an amnion, whilst the remains of the other foetal membranes (allantoic-sac, allanto-chorion and the greatly reduced yolk-sac) formed a folded membranous mass situated below, and in contact with the right side of the embryo (Pl. IX, fig. 41).

The egg-tooth, clearly visible in the intact embryo, was attached shortly behind the margin of the upper jaw and sloped downwards and backwards to terminate just in front of the mandibular symphysis. Its appearance suggested that its tip had been broken off, possibly as the result of use. It measured 0.26 mm. in length and 0.20 mm. in thickness at its base which appeared very broad.

In a recently hatched young one of *Echidna* (EBC) (12 mm. in G. L. in the contracted condition in which it was received), the egg-tooth is stated in our notes to have a length of 0.39 mm. and is described as consisting of an opaque basal segment, 0.10 mm. in length, supporting the tooth proper. The latter, 0.28 mm. in total length is translucent and distinguishable into a proximal thicker part and a distal spike-like tip, slightly recurved and about 0.10 mm. in length. The sections of EBB show that the apparent thick base of the tooth (and presumably also the basal segment of EBC) is formed by a prolongation of the epidermis

downwards around the base of the tooth and the shrivelled remains of the enamel organ (Pl. VI, fig. 23, *r.eo.*).

The enamel organ, not recognizable as such without knowledge of the earlier stages, is rather less degenerate than in *Platypus* WW and appears as an irregular ragged cellular membrane, loosely enclosing the proximal part of the tooth and in continuity with the downward reflection of the epidermis around its base (Pl. VI, fig. 23, *r.eo.* and *b.ep.*). Degenerate remnants of the enamel epithelium can still be made out, whilst the odontoblastic layer is reduced to a thin layer of small, mostly flattened cells. The pulp is still rich in capillaries.

The dentine has increased notably in thickness, now measuring 0.010 mm. Its outer surface is smooth and even and is formed by an extremely thin dark-stained layer; its inner surface is wavy and uneven.

In this *Echidna* embryo, the attaching bone and the premaxillae are of distinctly coarser texture and are more massively developed than they are in *Platypus* WW (Pl. VI, figs. 23, 24, *at.b.*, *m.px.*, *l.px.*). On the other hand, in correlation with the fact that the caruncle of *Platypus* is larger and more prominent than that of *Echidna*, it is interesting to find that the os carunculæ attains a distinctly larger size in the former than it does in the latter, as Wilson (1902, p. 730) has pointed out, whilst the ascending processes of the premaxillae exhibit a corresponding disparity in development in the two. When the medial laminae of the premaxillae which closely underlie the rostral cartilage in the snout region (Pl. VI, fig. 23, *m.px.*, *r.c.*) are traced forwards, they are found to turn upwards into the gap between the two short horns into which the above-mentioned cartilage splits at its anterior extremity. They lie in close contact with the medial surfaces of the horns and here form the ascending processes (Pl. VI, fig. 25, *a.px.*). They have a cranio-caudal thickness of about 0.05 mm., a vertical height of about 0.20 mm. and a transverse thickness of about 0.025 mm., and at this stage are very distinctly smaller in all their dimensions than the corresponding processes in *Platypus* WW. Turning back over the caudal margin of the gap above mentioned, they become continuous with the underside of the cranial extremity of the os carunculæ (Pl. VI, fig. 26, *a.px.*, *os.c.*).

The os (Pl. VIII, fig. 27, *os.c.*) has the form of an oval nodule, measuring 0.170 mm. in cranio-caudal length, 0.197 mm. in vertical height and 0.103 mm. in thickness and is thus much smaller than that of *Platypus* WW. Cranially its lower surface rests in a concavity on the surface of a median projection from the rostral cartilage (Pl. VI, fig. 23, and Pl. VIII, fig. 27, *r.c.*), whilst its caudal extremity lies in a corresponding concavity on the surface of the "prenasal" cartilage (? cartilage of the narial aperture) which fuses cranially with the rostral cartilage to form the just-mentioned median projection.

It looks as if in *Echidna*, the relatively weak support for the os provided by the ascending premaxillary processes is supplemented by that of the cartilages mentioned. In *Platypus* WW where these processes are much more strongly developed, the cartilage does not appear to play any supporting rôle.

Histologically the os (Pl. VIII, fig. 27, *os.c.*) differs from the premaxilla in the rather finer character of its trabecular matrix, which in both appears to be calcified, and in possessing smaller lacunae, mostly occupied by osteoblasts whilst many of the larger lacunae in the premaxillae are filled by embryonic connective tissue.



It is invested by a periosteal layer composed of spindle-shaped cells, internal to which is a discontinuous layer of osteoblasts but specially thickened and continuous along its upper margin.

It may be remarked that the relations of the ascending processes of the pre-maxillae to the os, in this embryo, do not, we think, afford support for the view that the latter arises by the fusion of the upper ends of these processes.

The caruncle itself, as noted above, is smaller and much less prominent in *Echidna* than in *Platypus*. Its epidermis (Pl. VIII, fig. 28) attains a thickness of 0.096 mm. over its apex, where it is thicker than over its sides and is well cornified. It consists of 4 layers: (a) a basal layer of columnar cells; (b) an intermediate layer with dispersed nuclei, 4 to 5 deep, in which cell-outlines are not recognizable in the apical region; (c) a granular stratum characterized by the presence of numerous coarse black granules; and (d) a laminated horny layer on the surface, 0.009 mm. in thickness.

Finally attention may be called to the occurrence in this embryo of small papilliform ingrowths from the buccal epidermis, on either side of the egg-tooth (Pl. VI, fig. 26, *d.l.*), the significance of which is obscure. The only suggestion we can make is that they are dismembered remnants of the dental lamina, the occurrence of which in *Echidna* has never been specifically described or figured, though Seydel (1899, p. 528) makes the bare statement that indications of a dental lamina and even of tooth-germs do appear in *Echidna*.

The ingrowths in question are seen at their best in Pl. VI, fig. 26, *d.l.*, on either side of the first trace of the egg-tooth in the sections. They occur in two sections, the ingrowth on the right side in the figure being knob-shaped and measuring  $0.021 \times 0.017$  mm., that on the left, a little less. A gap of 2 sections separates this pair from a cranial pair, whilst behind it, two small isolated ingrowths occur on the right and one relatively large ( $0.021 \times 0.015$  mm. in diameter) on the left. Behind the latter, a quite minute ingrowth occurs but is situated too far laterally to be in series with it.

In the lower jaw, two quite small isolated ingrowths are indicated.

#### *Stage VI.*

*Platypus WW* (twin of specimen W, the egg-tooth of which was described by H. L. Green (1930)).

Pl. VII, figs. 29–34; Pl. VIII, figs. 35–40.

The young were taken by the collector from the nest along with the mother and the egg-shells and are probably not more than two days old. Unfortunately we do not know whether they were found clinging to the hairs of the mammary areas of the mother or free in the nest.

The dimensions of WW are practically the same as those of W: viz. G.L. 16.75 mm., H.L. 6 mm.

In our original notes (dated 1900), the egg-tooth of W is stated to have measured 0.32 mm. in length and 0.19 mm. in breadth at its base, and is described as consisting of a thick basal portion and a thinner lancet-like apical portion, slightly curved backwards and tapering to a point, which presented a clear, translucent, horn-like

appearance. In WW, the egg-tooth measured about 0.35 mm. in length and 0.32 mm. in breadth at its base. It is noted in both cases that the measurements were difficult to make with accuracy; nevertheless the length of the tooth in W proves to be identical with that of the teeth in VV and GW.3, whilst the base-measurement of the tooth in WW is identical with that made on the sections.

The enamel organ is now in a very degenerate condition and is practically unrecognizable as such. It is seen in Pl. VII, fig. 29 and Pl. VIII, fig. 35 (*r.eo.*) as a more or less loose, irregular layer in continuity above with the epidermis and thicker on one side than on the other, which invests the neck of the projecting portion of the tooth and forms its apparent thick base. On the right side in Pl. VIII, fig. 35, what appears to be a remnant of the enamel epithelium (*e.ep.*) still persists as an irregular layer of degenerate cells, separated by a cleft from the upper portion of the dentine and in contact with the upward reflection of the epidermis. The dentinal shell of the tooth (*den.*) is almost three times as thick as that of GW.3, measuring about 0.012 mm. and as in previous stages, is directly continuous above with the massively developed attaching bone (*at.b.*). In favourable sections, the "dentine" now shows more definite evidence of structural differentiation than in any previous stage (Pl. VIII, fig. 37), since it is possible to distinguish in it three layers, viz. (*a*) an inner layer (*p.den.*) about 0.0032 mm. in thickness which has stained an intense dark blue tint; (*b*) a middle layer (*den.*) about 0.0068 mm. in thickness, which has also stained deeply but of a lighter blue than (*a*), and (*c*) an outer layer about 0.002 mm. or rather less in thickness, with a sharply defined, smooth outer contour (*en.*). It consists of a clear, refractive substance, which has failed to take the stain except for a thin surface-film which has stained fairly deeply.

As to the interpretation of these layers, we suggest that layers (*a*) and (*b*) together form the dentine, (*a*) representing the pre-dentine of preceding stages, now fully calcified, and that (*c*) constitutes the enamel. It occupies the site of the film-like layer we have described as present on the surface of the dentine in preceding stages but which we hesitated to identify as enamel. If it is really such, then it is enamel devoid of prismatic or other recognizable structure. Manifestly, it would be unwise to draw any conclusion from that fact but we may recall that enamel prisms are characteristic of mammalian enamel and do not occur in that of lower Vertebrates\*. Both Seydel (1899) and Green (1930) failed to find positive evidence of the presence of an enamel layer in the egg-tooth, though Seydel considered that it must be present because of the characteristic "weissliche Glanz" the egg-tooth exhibited, when it was examined intact in alcohol.

The pulp (Pl. VIII, fig. 35, *d.p.*) appears as a pale staining loose network composed of small spindle-shaped and stellate cells with anastomosing processes. It still contains small capillaries but has lost the extreme vascularity it possessed in earlier stages. The odontoblast layer has almost completely disappeared. It is

\* Dr. H. L. H. H. Green has examined the structure of the enamel and dentine of the molar teeth in the oldest mammary fetuses of *Platypus* available to him, and permits us to state that the enamel, when seen in tangential section, exhibits an unquestionable prismatic structure and that the dentine in section presents the characteristic radially striate appearance which is associated with the presence of dentinal tubules.



represented by the thin layer of degenerate cells seen in fig. 35, *od.*, internal to the apical portion of the dentine, and by isolated degenerate cells elsewhere.

The pulp, at this stage, is specially characterised by the occurrence in it of numerous large multinucleate osteoclasts (Pl. VIII, figs. 35, 36, *ocl.*) to the presence of which both Seydel (1899) and Green (1930) have called attention. They occur throughout the extent of the pulp but are specially abundant in its upper or basal part, at and above the level of the junction of the dentine with the attaching bone, and they also occur, outside its limits, in relation to the latter. In addition, young osteoclasts in the form of small oval to polygonal uninucleate cells, with deeply staining cytoplasm are present in numbers throughout the pulp.

The fully formed osteoclasts have the typical appearance and structure (Pl. VIII, fig. 36, *ocl.*). They are large (up to  $0.060 \times 0.034$  mm. in diameter) and of very varying outline, possess darkly staining cytoplasm and numerous small nuclei, each with a nucleolus, which are situated either peripherally in the cytoplasm or distributed through it. Sometimes they are provided with processes which may branch, brush-like. They occur free in the pulp but more frequently they lie in contact with the attaching bone, often in more or less distinct grooves in it and they are also to be found in contact with the dentine. Resorption of the attaching bone is in active progress.

The relatively massive development attained by its attaching bone is a striking feature of the monotreme egg-tooth, though in this stage, when the tooth has passed its best, it has already, as just stated, suffered considerable resorption. It arises as we have seen in direct continuity with the upper margin of the dentinal shell and is co-extensive with that. It accordingly takes the form of a continuous, thick and very irregular band, of an elongated oval shape, and about 0.23 mm. in cranio-caudal extent. In front, it connects up with the medial laminae of the premaxillae and with the lateral as well when these appear, whilst behind in the region of the root of the tooth where it attains its maximum development, its connection is mainly with the lateral laminae (Pl. VII, figs. 33, 34, *at.b.*). In this way, the bone provides a remarkably strong attachment and support for the egg-tooth, a condition which suggests that the latter is not merely a vestige but a structure of some functional importance in the life of the young Monotreme.

Whilst the attaching bone serves for the support of the egg-tooth, it is the premaxillae which participate in the support of that other most important temporary organ with which the young Monotreme is provided, viz. the caruncle or shell-breaker on the snout.

The relations of the attaching bone to the premaxillae and of the latter to the os carunculae which forms the internal skeletal support of the caruncle are illustrated in Pl. VII, figs. 29–34, showing a series of representative transverse sections through the snout region of the head. Fig. 34 (Pl. VII), the most caudal of the series, lies 0.02 mm. behind the termination of the dentinal shell of the tooth and shows the caudal extremity of the dentinal pulp almost completely enclosed by bone-trabaculae. Dorsally to it are the relatively small medial laminae of the premaxillae (*m.px.*), connected below with the massive lateral laminae (*l.px.*) which extend outwards as prominent wings and attain their maximum development at and just in front of the level of this section. Ventrally to the

pulp is a transversely disposed band of attaching bone (*at.b.*), connected at its lateral extremities with the lateral laminae. Behind the level of this section, the lateral laminae as well as the attaching bone rapidly become reduced in size, but the former continue back for a distance of 0.37 mm. on the right and 0.46 mm. on the left, and the latter, for a distance of 0.10 mm., before finally disappearing. The medial laminae also continue caudalwards and 0.07 mm. behind fig. 34 (Pl. VII) become connected ventrally by a massive anastomosis, extending over a length of 0.10 mm., and behind this rapidly become reduced to small processes which finally disappear, 0.22 mm. on the right and 0.24 mm. on the left, behind the level of that figure. They are thus distinctly shorter than the lateral laminae. Fig. 33 (Pl. VII) (0.08 mm. in front of fig. 34 (Pl. VII)), passes through the base of the tooth. The pulp is bounded below by a curved bar of dentine (*den.*) which is continuous laterally with the large irregular masses of attaching bone (*at.b.*). The connections of these latter with the now much smaller lateral laminae (*l.px.*) have been much reduced by osteoclastic resorption, whilst the connections of the medial laminae with the lateral are thicker.

In fig. 32 (Pl. VII) (0.07 mm. in front of fig. 33 (Pl. VII)), the mass of attaching bone on the right is connected with the now separated medial and lateral laminae, whilst on the left, it is connected with the medial only, by a thin partially resorbed strand. In the two sections next in front, both these connections have been resorbed. The lateral laminae (*l.px.*) are now much reduced in size and in fig. 31 (Pl. VII) (0.04 mm. in front of fig. 32 (Pl. VII)) have fused with the medial. The latter (*m.px.*), now thickened, immediately give origin to two stout prolongations (the left only (*a.px.*) complete in the figure), which run vertically upwards through the gap between the cranial wings of the marginal cartilage (*m.c.*) to become continuous with the base of the os carunculae (*os.c.*) (Pl. VII, figs. 31, 30, and Pl. VIII, fig. 38, *a.px.*). These prolongations are the ascending processes of the premaxillae. They lie more or less parallel with each other, on either side of the middle line, remain separate except for a slight cross-connection in one section, and have the form of laterally flattened bars or plates. Their dimensions are as follows: cranio-caudal width, about 0.09 mm., vertical height, about 0.34 mm., transverse thickness, 0.03 to 0.05 mm.

In fig. 31 (Pl. VII), it will be seen that the now much reduced masses of attaching bone have lost their original connections with the medial laminae as the result of resorption.

Traced forwards, the medial laminae gradually become reduced in thickness and appear simply as the lower ends of the ascending processes (fig. 30 (Pl. VII), which is 0.05 mm. in front of fig. 31 (Pl. VII)). In this figure, the connection of the attaching bone (*at.b.*) on the right is still fairly intact, whilst on the left, it has been resorbed, though it is again present in the two sections next in front.

The medial laminae and the ascending processes disappear 0.04 mm. cranial to fig. 30 (Pl. VII), and the masses of attaching bone fusing with each other across the middle line form an irregular thick band overlying the pulp and in continuity with the dentinal shell. In fig. 29 (Pl. VII) (0.08 mm. in front of fig. 30 (Pl. VII)), the cranial extremity (*at.b.*) of this band is seen in section, overlying the neck of the tooth.



*Os Carunculae.*

The os is now a very conspicuous structure in the sections through the snout (Pl. VII, figs. 29–34, *os.c.*). It has the form of an elongated ovalish nodule, with a cranio-caudal length of 0.58 mm., a maximum vertical height of about 0.54 mm., and a maximum transverse thickness of 0.28 mm. It reaches its maximum height and minimum thickness in its cranial half and its maximum thickness in its caudal half. To judge from its staining reaction, its matrix is calcified. It has stained fairly intensely of a deep blue tint which, however, is less intense and lighter than the dull and more opaque blue staining of the matrix of the ascending processes and the attaching bone. The bone is still increasing in size, for there is definite evidence of the continued formation of new matrix along its upper border which we recognized as its chief growth centre in GW.3, and, in much less degree, along its lateral surfaces.

In addition to the slight difference in staining reaction, mentioned above, the caruncular bone differs from that of the ascending premaxillary processes in its more open character, due to the abundance and large size of the lacunae, crowded with osteoblasts, present in it, some of them being exceptionally large (Pl. VIII, figs. 38, 39). The bone is invested by a layer of osteoblasts, much thickened along its upper border where the formation of new matrix is most active, and outside that by a thin zone of spindle-shaped periosteal cells.

Wilson (1900, 1902) to whom we owe the name “*os carunculae*”, was the first observer to give an account of its structure and relations, but in the relatively late mammary foetuses he had available for examination, the bone was in a more or less advanced stage of resorption by osteoclastic activity. He described (1902, p. 730) the premaxillae or rather their inferior lamellae as continuing “forwards into the prerostral region where they become attenuated and turn up dorsally into the prerostral notch and in front of the anterior extremity of the septal cartilage. Here the two osseous trabeculae (*px.*) fuse to constitute a remarkable nodule of bone (*o.c.*) which forms a skeletal foundation for the caruncle”. In his youngest specimen of *Ornithorhynchus* (D.C.L. 80 mm.), he states (1902, p. 731, and pl. xlii, fig. 22) that the interior of the bone is, in part, “hollowed away by osteoclastic absorption” and he describes also the existence of an area of what he believed to be hyaline cartilage, possibly partly calcified, situated “towards the dorsal portion of its interior”. That this area is a patch of “secondary” cartilage is apparent from the examination of the *os carunculae* in a still younger mammary foetus, *Platypus* X, with a D.C.L. of 56 mm.

In this latter specimen, the os has a cranio-caudal length of about 0.56 mm. and (0.20 mm. behind its cranial extremity), a maximum vertical height of 0.88 mm. and a maximum transverse thickness of 0.42 mm. Comparison of these measurements with those of the os in WW. given above, reveals the rather unexpected fact that in the interval when the caruncle has ceased to have any functional value and has itself become greatly reduced, the os has undergone an increase of about one-third in height as well as in thickness.

Over its cranial third or thereabouts, the os consists of a bony shell, much thicker along its ventral border than elsewhere, composed for the most part of compact bone, which encloses a central core of “secondary” cartilage, the cells

forming the more dorsal portion of which, are specially characterized by their thick, deeply staining capsules. About 0.20 mm. behind the cranial extremity of the os, a patch of spongy bone similar to that forming the os in WW makes its appearance below the cartilage. It extends back through four sections and then begins to undergo resorption. Osteoclastic activity also spreads to the adjacent bony shell with the result that over the caudal third of its extent, the os is represented by a dorsal fragment in the form of an incomplete bony ring enclosing a mass of "secondary" cartilage, which is widely separated from a ventral fragment with which the ascending processes of the premaxillae are in continuity. These latter are still complete but they are thin and in process of resorption.

Wilson (1902) states that in his pouch-foetus of *Echidna* (approx. D.C.L. 12.5 cm.) the premaxillary trabeculae (ascending processes of the premaxillae) extend into, but not through the shallow prerostral notch, so that their original connection with the os carunculae has entirely disappeared.

We may conclude accordingly that the precocious formation of these processes in the Monotreme is definitely to be correlated with the presence of the caruncle and its associated supporting nodule. They clearly serve no other purpose than to act as struts for the support of the caruncle.

The caruncular epidermis (Pl. VIII, fig. 40) reaches a thickness of 0.094 mm., its surface layer being well cornified. It consists of a basal layer of irregularly cubical cells, an overlying pale-staining zone composed of about five layers of flattened cells with oval nuclei, which merges into a deeply staining zone, composed of from five to six layers of flattened spindle-shaped cells, with dark granules in their cytoplasm. This granular zone gives place rather abruptly to a superficial lightly staining, cornified layer, 0.017 mm. in thickness, which is laminated and contains sparse flattened, degenerate nuclei.

#### B. ON THE OCCURRENCE OF VESTIGES OF THE EGG-TOOTH AND THE CARUNCLE IN THE MARSUPIALIA.

##### *Trichosurus vulpecula.*

The rudiment of an egg-tooth papilla is found to be regularly present in embryos between 13.5 mm. and 15.5 mm. in length. This takes the form of a small papilliform condensation of the mesenchyme which has indented the buccal epithelium, producing in it a well-marked basin-like depression, in the midline, immediately ventral to the site of origin of the premaxillae. (Pl. IX, fig. 44).

In the 13.5 mm. stage (Pl. IX, fig. 45), the layer of cells forming the basal layer of the buccal epithelium, immediately external to the basement membrane, is continuous round the concave basin enclosing the papilla. The buccal epithelium which is about 0.1 mm. in thickness at each side of the papilla, is 0.05 mm. thick at its apex. On each side of the papilla, the buccal epithelium is stratified and the basal layer of cells is underlain by a layer of similar cells. This sub-basal layer is, however, not continuous round the concavity occupied by the papilla, where the cells are more irregularly and loosely arranged. Immediately to the side of the papilla, there is beneath the basal layer a loosening of the cells which suggests comparison with the space which is eventually formed in this position in *Platypus*.



The papilla is formed by mesenchyme cells which are somewhat more densely arranged than in the sub-epithelial mesenchyme surrounding it. There is, however, in the papilla no regular arrangement of a layer of "odontoblasts".

A further feature that is worthy of notice is the presence in the sub-epithelial mesenchyme, in the immediate vicinity of the papilla, of numerous large capillaries.

At the 14 mm. stage (Pl. IX, fig. 46), the papilla shows a certain advance in histogenesis. The mesenchyme cells of the papilla are more closely packed and the capillaries in the surrounding mesenchyme are even more numerous and more closely associated with it. In the buccal epithelium, a concave stratification of cells is now evident immediately below the papilla, where the cells are distinguishable as flatter than in the ordinary regions of the epithelium on each side.

At the 15 mm. stage (Pl. IX, fig. 47) the rudiments of the premaxillary bones are ossified and are seen to lie just above the egg-tooth papilla, one on each side of the midline. The papilla itself shows the same densely packed mesenchyme cells, and is slightly smaller than in the previous stages. The buccal epithelium on the other hand is slightly thicker, and a marked stratification of cells under the papilla may be seen. Its basal layer exhibits a considerable degree of specialization as if it were differentiating to form an enamel epithelium, whilst below it, the cells of its intermediate layer show a laminar concentric arrangement around the basin-shaped depression occupied by the papilla. Capillaries are even more strongly developed.

No trace has been found of the deposition of dentine by the mesenchyme cells of the papilla, nor of enamel by the epithelial cells lining the cup of the papilla, and, indeed, it is hardly to be expected that any should be formed.

Broom has described in the pouch-young of G.L. 14 mm. (1909, p. 202) the premaxillary bones as showing "an ascending internasal process, as in reptiles. The process is not ossified, but the strand of differentiated cells, perhaps degenerate osteoblasts, can be easily traced into the region to be occupied by the "nasal bone". We have been able to verify this statement, and, as will be seen below, similar conditions have been found by us in other species of Marsupials: viz., *Didelphys aurita*, *Caluromys philander* and *Perameles nasuta*.

*Phascolarctos cinereus.*

At the 16.5 mm. stage (Pl. X, fig. 48), the appearance of the rudiment of the egg-tooth papilla is similar to that in early stages of *Trichosurus*; the position is identical, in the midline, immediately beneath the level at which the premaxillary bones will subsequently ossify. In *Phascolarctos* the papilla is comparable in size to that of *Trichosurus*, about 0.1 mm. in diameter, but its basin in the thickness of the buccal epithelium is a little less deeply excavated. On each side of the papilla, at a distance of 0.25 mm. from it, this epithelium projects inwards to form the anterior end of the dental lamina. The mesenchyme cells forming the papilla are very densely packed and the sub-epithelial mesenchyme shows many large capillaries.

At the 18 mm. stage (Pl. X, fig. 49) the premaxillary bones are ossified and they show a structure of great interest. From the medial border of each premaxillary

bone, a bony spicule or attaching-bone trabecula projects straight down to terminate close to the margin of the egg-tooth papilla, as if it were a support for the absent egg-tooth, in a manner precisely comparable to that which is found in the Monotremes.

*Didelphys aurita* (Pouch-young, H. L. 8.5 mm.).

The pouch-young of *Didelphys aurita* which we have examined do not show the rudiment of the egg-tooth papilla, but they reveal the presence of another structure which is closely associated with the presence of an egg-tooth. This is the vestige of the median ascending process of the premaxillary bones. This process is here represented by a median strand of dense connective tissue which rises upwards from the antero-medial corners of the premaxillary bones, and projects dorsally immediately in front of the anterior wall of the nasal capsule, between the anterior cupulae (Pl. X, fig. 50, *md.c.*). Dorsally to the roof of the nasal capsule, this strand of connective tissue curves posteriorly and ends in a thickened knob which may be regarded as the vestige of the os carunculae of the Monotreme (Pl. X, fig. 51, *c.os.c.*), and which Denison and Terry (1921) found to ossify as an independent nodule of bone in *Caluromys*.

*Caluromys philander* (Pouch-young, H.L. 8.25 mm.).

As in *Didelphys*, no trace of an egg-tooth papilla has been found in *Caluromys*, but this species shows the same condensation of connective tissue representing the vestige of an ascending process of the premaxillary bones (Pl. X, fig. 52, *md.c.*). The pouch-young stage available for study was not suitable for verification of Denison and Terry's (1921) statement that an ossified os carunculae occurs in this species, but what we regard as a mesenchymatous vestige of the os is seen in Pl. X, fig. 53 (*c.os.c.*)

*Perameles nasuta*.

The new-born *Perameles* shows a similar condensation of connective tissue representing the ascending processes of the premaxillary bones.

#### DISCUSSION.

The egg-tooth in Reptiles and in Monotremes is found in association with a number of characteristic features. In the first place, there is the papilla of the egg-tooth itself. Next, the premaxillary bones develop bony processes which become attached to the dentine of the egg-tooth, either directly or by way of independently arising trabeculae of membrane bone, and provide it with a firm anchoring. Then the premaxillae are often found to possess well-developed ascending processes, often fused in the midline, which rise dorsally in front of the nasal capsule. Lastly, in Monotremes, there is an os carunculae which surmounts the ascending processes, becomes fused with them, and provides a firm skeletal base for the caruncle.

Representatives of all four of these features are found in the Marsupialia, where they can only be regarded as vestiges of structures which served as adaptations to enable the embryo to free itself from the egg-membranes and egg-shell in their oviparous ancestors. Such vestigial structures take their place beside those other features discovered and described by Hill (1910) such as: the large size of the



uterine ovum relatively to those of the Eutheria ; the presence outside its investing zona, of a layer of albumen and a shell-membrane which increases in thickness in the uterus, like that of the Monotreme ; and its relative richness in deutoplasmic (yolk) material, part of which is extruded before cleavage begins. All of these features likewise point to the condition when the ancestors of the Marsupialia were oviparous.

The structures and features here described therefore represent vestiges which have been handed down from ancestors in the remote past. It may be of interest to make an attempt to estimate the length of time during which these functionless vestiges have persisted. In *Eodelphis* (Matthew (1916), Simpson (1928) ) we have a genus which, although Cretaceous in date, was already typically Marsupial and it is reasonable to assume that it did not differ from the present Marsupialia in its mode of development. The age of the strata in which *Eodelphis* is preserved can now be estimated with some degree of accuracy, and is found, so Prof. D. M. S. Watson informs us, to be of the order of seventy-five million years.

### C. CONCLUDING REMARKS.

#### 1. *Development of the Egg-Tooth.*

Our observations confirm the conclusion of Seydel and Green that the egg-tooth of the Monotreme takes origin, like the transient toothlets of Reptiles and the lower jaw teeth of Urodeles, as a mesodermal papilla which directly indents the buccal epithelium and which in its continued growth, carries the latter before it to form its external covering. But they enable us to go further and to show that from that epidermal investment there is differentiated a well-developed enamel organ, similar to that of the Reptilian toothlet and comprising all the parts typically found in such an organ (enamel epithelium, stellate reticulum and stratum intermedium, outer enamel epithelium). The superficial cells of the mesodermal (dentinal) papilla differentiate to form a layer of odontoblasts, under whose agency and apparently on the basement membrane as a basis, there is laid down a layer of dentine, which, cap-like, invests the papilla down to its base and slowly increases in thickness to a maximum of about 0.012 mm. The dentine appears perfectly homogeneous, and so far as we have been able to observe, is devoid of dentinal fibres.

On the surface of the dentine, next the enamel epithelium, there is evidence of the presence of a very thin refractive layer, which, film-like in the earlier stages, attains its maximum thickness of about 0.002 mm. in *Platypus* WW. We have suggested, in view of the presence of a well developed enamel epithelium, that this may be a layer of enamel and have pointed out that if it be such, it is enamel devoid of prismatic structure and so differs from that of other mammals and agrees with that of lower vertebrates.

The dentinal papilla attains a high degree of vascularity but no capillaries ever penetrate into the stellate reticulum of the enamel organ. In compensation for this lack of a vascular supply, a conspicuous ring-like space is present in the stellate reticulum at the base of the enamel organ. It is separated from the overlying capillaries by a thinned-out strip of the buccal epithelium through which diffusion can readily take place, and so probably functions as a nutritive or lymph channel.

One of the outstanding features of the egg-tooth is the remarkable development attained by the bone serving for its attachment and support. This bone arises in direct continuity with the dentinal shell of the tooth and independently of the premaxillae with which, however, it soon becomes continuous.

In our oldest stage (Platypus WW. recently hatched), the egg-tooth has passed its zenith and resorption of its attaching bone is in active progress.

## 2. *Morphology of the Egg-Tooth.*

Green (1930), with great acumen considering the meagre data he had at his disposal, pointed out that "in its form and general relationship to other tissues this tooth [the egg-tooth] entirely resembles the dentinal shell described by Wilson and Hill (1907) as an undoubted remnant of the milk tooth ("dv.") of *Ornithorhynchus*" (p. 517). With the substance of this statement we are in entire agreement since we also have arrived at the conclusion that the egg-tooth is to be regarded as belonging to the same tooth-generation as the vestigial calcified toothlets, which the authors named observed in their specimen Delta (D.C.L. 80 mm., Pl. X, figs. 4 and 5) and which they regarded as belonging to an earlier tooth-generation than that to which the more posteriorly placed enamel organ ("W") belonged, and as the deciduous predecessors of the tooth germs ("V") of the later stage, Beta. Our contention then, is that the egg-tooth and the vestigial toothlets are serially homologous structures. But we would point out, *contra* Green, that nowhere in their paper do Wilson and Hill refer to the toothlets in question as "milk teeth". The milk teeth of mammals are the product of the dental lamina and these toothlets certainly are not. They found the toothlets present on both sides of the upper jaw, slightly in front of the premolar tooth-germ ("W"), but only doubtfully present in the lower jaw. In their figs. 4 and 5, Pl. X, the toothlet is seen to project partly into the oral epithelium, partly into the labial side of the neck of the dental lamina so that its superficial portion is enclosed in a cap of epithelial cells derived from these structures. Its deeper or root portion is simply embedded in the connective tissue. Below the epithelial cap is a thick layer of dentine, connected with an irregular mass of dentine in the pulp.

Subsequently Green himself (1937) in an earlier stage of Platypus (Platypus X, D.C.L. 56 mm.) encountered the same toothlets in the pre-molar region of the dental lamina, but in a much less degenerate condition than those of Wilson and Hill's specimen Delta. They are present according to Green in both jaws, but those of the lower jaw are devoid of dentine. The upper jaw toothlet (well seen in his figure 28, pl. 34), indents the buccal epithelium immediately to the lateral (labial) side of the neck of the dental lamina, as in Delta, and consists of a mesodermal papilla, invested by a thin shell of dentine and an enclosing enamel organ, differentiated directly from the buccal epithelium, and comprising a well-marked enamel epithelium, a stratum intermedium, a stellate reticulum and a rather indefinite enclosing layer furnished by the middle zone of the buccal epithelium and the labial wall of the dental lamina. We reproduce a photomicrograph of this toothlet in our fig. 42, Pl. IX. Comparison of this figure of the toothlet ("dv") with our figures of the egg-tooth leaves no room for doubt of the essential identity in the developmental and structural relations of the



two. Both take origin from a mesodermal papilla which indents the buccal epithelium, and in both the enamel organ is differentiated directly from the latter, without the intervention of a dental lamina. The differences between them in size and position find their explanation in the fact that the egg-tooth is a structure of high functional importance in the economy of the young Monotreme and so has persisted as a well-formed hypertrophied tooth, while the toothlets represent the vestigial remnants of the dentitional series to which it (the egg-tooth) belongs and which was replaced in the ancestral Monotreme by the tooth-series developed from the internally situated dental lamina. It is perhaps deserving of mention that Wilson and Hill in their later specimen, *Platypus Beta*, recorded the existence of an undoubted vestigial toothlet (designated " $dy^2$ " in their nomenclature) underlying the posterior region of the antero-internal cusp of the upper molar tooth (" $y$ "), well to the labial side of the residual dental lamina. It lies adjacent to the buccal epithelium, between that and the outer layer of the enamel organ which it slightly indents (Pl. XII, figs. 9 and 11). Structurally the toothlet consists of a ring of dentine enclosing a connective tissue pulp and surrounded by a quite definite layer of radially arranged enamel epithelial cells, outside which is a connective tissue capsule, representing the stellate reticulum. The authors regarded this toothlet as being serially homologous with the concentric epithelial nodules which occur in front of, and behind it, in relation to the internal cusps of the upper and the external cusps of the lower molars. This view, however, Green (*loc. cit.*) has shown to be untenable. Green was unable to find any trace of this toothlet in any of the specimens he examined and dismisses it as being "adventitious" and "peculiar to one side of the jaw in this particular specimen". Nevertheless its occurrence is of significance since it suggests that the toothlets formerly extended right back into the molar region of the jaw.

If we turn now to the Reptilia, we find that Röse (1893) was the first to show that in the embryo of the Crocodile, the earliest teeth to appear (forming his "erste Zahnserie") take the form of small transitory toothlets, each of which arises from a mesodermal papilla which indents a localized thickening of the buccal epithelium, distinguishable before there is any trace of the papilla. The toothlets so closely resemble the placoid scales and early teeth of the Selachii in their development that Röse termed them "placoiden Schleimhautzähnen" or "placoiden Zähnchen". He showed that they lie labially to the definitive dental lamina which appears later and that they acquire dentinal caps whilst still projecting into the buccal epithelium. The deep layers of the Malpighian stratum of the latter later furnish an enamel organ, provided with a distinct stellate reticulum, for the toothlet. They finally undergo resorption before the young hatch out from the egg. We have been able to confirm Röse's account of the relations of these structures in the Crocodile embryo. Subsequently similar toothlets were described in other Reptiles, by Röse (1894) in *Vipera*, Leche (1893) in *Iguana*, Harrison (1901) in *Sphenodon* where they actually erupt and are shed, Bolk (1912) in *Lygosoma*, and especially by Woerdeman (1919) in his valuable studies on the development of the teeth of Reptiles. This author concludes from his detailed observations on *Gongylus* and *Crocodilus* (and in accordance with Bolk's views) that the toothlets do not form a single tooth-generation as

Röse held, but are arranged in two rows or Odontostichies (designated  $O_I$ ,  $O_{II}$ ) which develop successively, the members of adjacent rows alternating with each other. He regards this arrangement as the persistence of an ancestral condition. His description of the development of the toothlets themselves agrees essentially with that of Röse. They appear first as localized epithelial thickenings ("gemmae") in the "Zahnepithelfeld" which become indented by "freie Papillen", and later, by the "Operculization" of that field, the dental lamina is formed on their lingual side. They each develop an enamel organ and a dentinal cap and later, sinking into the mesoderm, undergo resorption *in situ*.

Woerdeman fails to confirm Röse's statement that the toothlets possess a "Cementsockel" of delicate bone-trabeculae which are in continuity with the dentine. Woerdeman finds it difficult to believe that these toothlets are transitional forms and thinks it more probable "dass die Abortivzähne der Reptilien Rudimente von Schleim-Hautzähnen sind, welche bei ihren Ahnen funktioniert haben" (p. 223).

If, as we believe, the vestigial Monotreme toothlets are the homologues of these Reptilian toothlets, then they must be regarded as phylogenetically extremely ancient structures, and the same holds for the egg-tooth. Seydel (1899), though he had no knowledge of the existence of an enamel organ in the Monotreme egg-tooth, recognized the general similarity in the mode of development of the latter and of the transitory toothlets of the Crocodile as described by Röse. He regarded "den Eizahn von Echidna als den Rest einer alten im Allgemeinen längst unterdrückten Zahngeneration".

Green (1930) also emphasized the similarity in question and provided a figure (Pl. I, fig. 6) of an early developmental stage of a Crocodile toothlet, showing the mesodermal papilla, invested by a dentinal cap, directly indenting the oral epithelium. He concluded that the Monotreme egg-tooth "structurally represents an extremely old phylogenetic type of tooth-evolution".

### 3. The Egg-Teeth of the Squamata.

Turning now to a consideration of the observations of Woerdeman on the development of the egg-tooth in the Squamata, we find that the Ophidia alone possess a primarily median, unpaired egg-tooth, which according to the author, represents the antero-median element, common to the two second rows (Odontostichies) of toothlets, which he designates  $O_{II}$ . The Lacertilia (with the exception of the Geckotidae) also possess a median egg-tooth but here it is only secondarily median. In some genera (*Gongylus*, *Mabouya*), two egg-teeth primordia, para-median in position, are recognizable. They represent the most anterior elements of the 2nd rows ( $O_{II_1}$ ), but the right  $O_{II_1}$  increases in size, moves to the middle line and forms the egg-tooth, whilst the left  $O_{II_1}$  degenerates. In other genera (*Cyclodus*, *Lacerta*, *Lygosoma*), the left  $O_{II_1}$  apparently fails to develop, the right  $O_{II_1}$  appears to the right of the middle line, grows in size, moves into the median plane and forms the egg-tooth.

Lastly, in the Geckotidae (*Ptychozoon*, *Gecko*), paired egg-teeth are present which are derived, according to the author, from the anterior members of the first row of toothlets ( $O_I$ ).



It would accordingly appear that the median egg-tooth and the paired egg-teeth of the Squamata are formed by the persisting and hypertrophied anterior member or members of either the first or the second rows of toothlets which develop from what Woerdeman terms "freie Papillen".

We have been able to confirm Woerdeman's account of the relations of these structures in *Tropidonotus*, *Lygosoma*, *Lacerta* and *Hemidactylus*.

Confirmation is thus afforded for our conclusion that the Monotreme egg-tooth and the vestigial calcified toothlets are serially homologous. It should be noted, however, that there is one apparent exception to the above generalisation inasmuch as Woerdeman, with reference to *Gongylus*, writes (p. 235): "Aber überdies werden die Eizahnanlagen von *Gongylus* nicht als freie Papillen gebildet, sondern an einer Zahnleiste. Sie gehören also nicht zur ersten Zahnserie" (of Röse) and he concludes "der Eizahn ist der alleinig übrigbleibende Zahnkeim der rechten zweiten Zahnreihe". We must confess we found the first of these quotations somewhat disturbing but were reassured when we examined his fig. 25, Taf. VII. In that figure the primordium in question,  $O_{II_1}$ , is seen in the form of a well developed toothlet, situated on the labial side of the dental lamina and directly above the dental groove. So far as we can judge, it differs in no essential way from the toothlet ( $O_{II_1}$ ) illustrated in Taf. VII, fig. 24a, about the nature of which there is no question. We might here call attention to the remarkable similarity of Woerdeman's fig. 25, which we reproduce here as our fig. 43 (Pl. IX), to our fig. 42 of the calcified toothlet of *Platypus* X, described by Green (1937), to which we have referred above.

Woerdeman is of opinion that the egg-teeth in the various genera of Reptiles are not homologous. This we think is an extreme view. The toothlets whether they belong to Odontostichy I or Odontostichy II agree in their mode of development and structure. It is true that they differ slightly in age and position but that surely does not invalidate their homology. The teeth on the jaws of a Selachian differ also in age and position but no one, we imagine, would deny their homology on that account.

The whole trend of recent comparative and experimental work on homology has been to show that it is necessary to recognize the possibility of variation in time and place of origin of structures which are "made" *de novo* in each generation, and which can show considerable differences without necessitating the abandonment of the view of their common descent. Many examples of this principle have been given by de Beer (1938). Here attention may be called to the work of Butler (1937, 1939), more particularly since it is concerned with the homology of teeth. Butler has shown that the differentiation of Mammalian teeth into incisors, canines and molars is the reflection of the existence of regional morphogenetic fields which may vary in their extension along the jaws. Dissimilarity of position between otherwise similar teeth cannot be regarded as a bar to their community of origin in evolution. In a similar way we would suggest that formation of the egg-tooth from Odontostichy I or Odontostichy II does not invalidate the view that egg-teeth so-formed have community of origin.

If it be granted that the toothlets in the two rows are homologous, then it follows that their hypertrophied anterior members which form the egg-teeth are also homologous.

#### 4. *Egg-Tooth and Caruncle : Occurrence and Function.*

The fact that the Monotremes are unique amongst the Amniota in the possession of both a caruncle and an egg-tooth appears to have escaped the notice of all previous writers. The existing Reptiles, as is well known, are provided with either the one or the other, but never both. If the Monotremes are derived from an ancestral Reptilian stock as all the evidence goes to show, then we must presume that the ancestral Reptile also possessed both structures, unless we are to hold that the caruncle of the Monotreme has nothing to do with that of the Reptile and is an independent acquisition, the result of developmental parallelism.

Röse (1892) was the first observer to direct attention to the distribution of these two structures amongst the Reptilian Orders. He pointed out that those Reptiles in which the egg-shell is parchment-like and little calcified possess an egg-tooth, an instrument well adapted by its pointed and forwardly directed character to pierce or tear open the thin shell, as Goldstein (1890) showed. On the other hand, those in which the shell is thick, strongly calcified and resistant possess a caruncle, a hard horny structure, well adapted to bring about the cracking of the brittle shell by being persistently tapped against it.

The former group which has retained the egg-tooth comprises only the Squamata (Lacertilia, Ophidia). The latter group which has retained the caruncle, includes the remainder of the Reptiles (Rhynchocephalia, Chelonia, Crocodilia) and the Birds.

Sluiter (1893) did not accept Röse's conclusions on the ground that amongst the Chelonia, the tortoises possess thick, hard shells, whereas in the marine turtles the shell is soft and leathery, but we attach little weight to this objection since the latter condition may well be secondary.

In the ancestral Reptile, presumed to possess both structures and a hard shell, the function of the caruncle was no doubt the same as in existing hard-shelled Reptiles, viz., to crack the shell, whilst the primary function of the egg-tooth, we may suppose, was to enable the young one to free itself from its foetal membranes, in particular the amnion and the allanto-chorion. When, in the Squamata the soft shell replaced the hard shell, the caruncle disappeared and the egg-tooth, whilst retaining its primary function, acquired an additional secondary function, that of piercing and ripping open the shell.

That the egg-tooth in recent Squamata does function in this way was first shown by Weinland so long ago as 1856 in his paper on the structure of the egg-tooth in *Tropidonotus*. Indeed he was the first observer to employ the designation "egg-tooth"; "Diesen Zahn könnte man am besten Eizahn nennen" (1856, p. 91). He described how the young snake emerges through a slit made by the egg-tooth in the leathery shell, the slit being  $\frac{3}{4}$  inch in length and possessing sharp edges as if it had been cut with scissors and not rent by pressure. He relates also that when holding the wriggling young snake in his hand it scratched his finger with its egg-tooth!

Goldstein (1890) also described the hatching phenomena in *Lacerta vivipara*. He relates that he could see through the transparent uterine wall and the thin shell how the young one tried to stretch the shell by propping itself against it with its snout and tail and how it only succeeded after several attempts in piercing



the shell with its egg-tooth. The latter, he states, is lost in the process. Recent observations on the hatching of the Python, made with the assistance of a film taken by Mr. Douglas Fisher, have enabled us to establish that the leathery shell is slashed by the egg-tooth as by a razor, some half-a-dozen times. The young Python which fills its shell very fully, is thus able to emerge with ease.

Some observations of great interest from the present point of view have been made on *Anguis fragilis* by Dr. A. Malcolm Smith, who, with his characteristic generosity, has permitted us to refer to them here, although he has not yet published them. Dr. Malcolm Smith writes: "I had killed a slow-worm that I knew was going to give birth to young in a day or two, in order to investigate a problem concerning the osteodermal sheath and pregnancy, when I suddenly realized that I had lit upon a means by which I could watch the young emerge from their "shell". I removed them one by one in their envelopes and watched the liberation, which was done in a few minutes. I saw it four times and the method adopted was the same in each case. . . The young are fully developed and still alive so that I feel sure that what I witnessed was the normal method of liberation. The membrane is sufficiently transparent to enable one to see exactly what the embryo is doing. The head was repeatedly thrust forward until finally the membrane was pierced and the young one crawled out head first. There was no side to side movement of the head and no struggling by the body. The operation once it was begun did not take more than a minute. It is I think much what one would expect considering the poor development of the egg-tooth in the slow-worm, and I rather incline to the view that in the lizards the tooth is a piercing organ, to be followed by the snout, rather than a slashing organ. From what I have seen of the geckos they do not slash. The Americans claim that some of their terrapins liberate themselves with their claws".

But why, it may well be asked, did the hard-shelled Reptiles discard the egg-tooth if it originally was of value in assisting the embryo to free itself from its foetal membranes and how is this effected in the Reptiles in question?

In attempting to answer these questions, we would point out in the first place that there is some evidence that the egg-tooth can be dispensed with when it is no longer of functional use. Haacke (1885) has stated that the Australian stump-tailed lizard (*Trachydosaurus asper*) lacks an egg-tooth at the time of birth. This lizard is viviparous, with usually a single embryo in each uterus. The full-grown young one is very large, about half the length of the parent, and is doubled up in the uterus (McCoy, 1885), being plainly visible through its thin wall and the thin membranes investing it. To rupture the latter at the time of birth, the young lizard, so Haacke says, only needs to straighten itself out. He also mentions that in *Cyclodus boddaertii* (= *gigas*), which is also viviparous, the young one likewise lacks an egg-tooth. Woerdeman, however, states that in embryos of this same species, the egg-tooth is present and formed by right  $O_{II}$ , the corresponding left toothlet being absent. It is possible, of course, that the egg-tooth of the embryo is shed or resorbed before the birth of the young one, but confirmation of these observations of Haacke's is highly desirable.

In the case of the viviparous Reptile or the Bird, we may recall that the young one with its membranes, at the time of hatching, practically fills the shell and

that it is more or less flexed or folded. When, prior to hatching, it becomes more active and begins to straighten itself out, it can obtain considerable purchase by propping itself against the shell as Goldstein (1890) has observed. Now the chick just before hatching is described as raising and extending its head so that the membranes are pierced and the beak is inserted into the air chamber, and doubtless the same or comparable movements are carried out by the young Reptile. In the soft-shelled forms, the piercing and rupture of the egg-membranes would be effected with the aid of the egg-tooth. Then continuation of reflex muscular activity, by producing alternate movements of the head either in the fore and aft or lateral direction, would enable the egg-tooth to pierce or rip the shell. In the case of the hard-shelled species, the straightening out of the embryo and the extension of the head would result in the mechanical rupture of the membranes, and contact of the caruncle with the shell might be supposed to induce the spasmodic muscular contractions which, by forcibly raising the head, enable the caruncle to carry out its function of cracking the shell. Keibel (1912) has stated that in the Chick, the chief muscle concerned in the tapping action of the caruncle is the *musculus complexus* (*M. semi-spinalis capitis*). These considerations, it must be admitted, do not take us beyond the already obvious conclusions that an egg-tooth is essential in the soft-shelled species, and a caruncle in the hard-shelled forms and that the latter can rupture their egg-membranes without the aid of an egg-tooth. If they originally possessed one, it came to be superfluous and so has been suppressed.

The circumstances of the young Monotreme, just prior to hatching, differ considerably from those of the young Reptile at the same stage. We have recorded (*ante*, p. 516), that our *Echidna* embryo, EBB, was found, when the shell was opened to have lost its amnion, whilst the egg-tooth appeared to have lost its tip. The condition of the shell itself unfortunately is not described in detail in our notes. Its approximate diameter is given as  $17 \times 13.5$  mm. and it appears to have been somewhat distorted and collapsed and possibly cracked. The possibility that the shell normally becomes shrunken and dented at this stage should not be overlooked. According to Burrell (1927, p. 180) the shell of the *Platypus* egg frequently becomes dented as incubation proceeds. The remainder of the foetal membranes in EBB, comprising the greatly reduced yolk-sac, the allanto-chorion and allantois, together formed a shrunken, membranous mass, situated below, and to the right side of the embryo. Consequently it occupied only part of the space inside the shell, and if the latter were fully expanded, it is difficult to see how the embryo could obtain any purchase at all on its smooth inner surface, when the time came to use its caruncle.

Furthermore the trunk of the young Monotreme, unlike that of the young Reptile, is at this stage already fairly straight, with the head flexed at right angles to it. Its fore-limbs are powerfully developed, being far in advance of the hind limbs, and the digits are armed with strong recurved claws. As to the capacity of the young one for movement, we may suppose it is capable at least of raising and lowering its head, moving its arms and possibly opening its mouth.

Again, the egg-tooth, by its relatively small size and its backwardly recurved form contrasts sharply with that of the Lizard or Snake. In view of its size and



its position, tucked away under cover of the upper lip, it does not strike one as a particularly efficient weapon, but if its only function is to produce a rent in the thin amnion, it probably suffices, with or without the help of the forelimbs. The allanto-chorion is connected with the yolk-sac by a narrow, very thin strip of chorion which would readily rupture on any shrinkage of the yolk-sac, so that the young one has a quite simple task in freeing itself from its membranes\*.

Much more difficult to understand is how it makes the perforation in the shell through which it escapes. Burrell (1927) who examined numbers of empty egg-shells of *Platypus* states that he always found them in a collapsed state in the nest and that the aperture of escape takes the form of a ragged rent usually situated at one end of the shell. In regard to the method of escape, he writes (*loc. cit.*, p. 183) "Whether helped by an egg-tooth or not, it is probably an easy matter for a *restless muscular creature* like the platypus embryo to break through the *thin* shell, using the caruncle as a point of resistance against the pull of the fore-paws" (italics ours). We do not find this explanation very illuminating. Only if the shell had previously become in some degree shrunken and folded can we picture the young Monotreme obtaining the purchase on the shell necessary to enable the caruncle and fore-limbs, one or both, to come into effective action. In any case we think the caruncle and the fore-limbs are the structures concerned in bringing about the perforation of the shell and the latter certainly are the effective agents in enabling it to escape, once an opening has been made.

#### 5. *The Caruncle in Monotremata and Sauropsida.*

Although Aldrovandus (1597) may have been the first to describe it, John Hunter is the first English observer, known to us, to take note of the caruncle of the Chick. In the Hunterian Manuscript (Desc. & Illustr. Cat. Museum, R.C.S. Vol. 5, p. xxxi) occurs the following sentence: "The little horny knob [pl. 76, figs. 17 and 18, b] at the end of the beak with which it breaks the shell when arrived at the full time and makes its escape, is also gradually forming into a more regular and determined point, the progress of which is seen from the first figure to the sixth." He thus long antedated W. Yarrell who in 1826 communicated a paper to Vol. 2 of the *Zoological Journal* on the presence of "the small horny appendage to the upper mandible" in a number of birds (Chick, Pigeon, Ducks and Geese). R. Owen (1835) provided the first description of the caruncle in the Monotreme in his paper on the young of *Ornithorhynchus* (see also his article on the Monotremata in Todd's *Cyclopaedia of Anatomy and Physiology*; Vol. III 1839-47). He described it in his younger specimen with a D.C.L. of 93 mm. as "a minute fleshy eminence lodged in a slight depression", situated "on the middle line of the upper mandible and a little anterior to the nostrils", and in the explanation of his fig. 8 (pl. 33), he refers to it as the caruncle. He regarded

\* Possibly also the egg-tooth is of use, along with the forelimbs, in enabling the young one to cling to the hairs of the mammary area, during the first day or two of its life. Kershaw (1912) relates that in examining a live female *Platypus*, taken from the nest, he found a very small young one (about 15 mm. in length) "so securely attached to the skin of the abdomen as to require a little force to detach it". The second young one present dropped off in lifting the mother. According to Burrell (1927, p. 183), the egg-tooth is no longer present in the young one 18 mm. in length.

it as " obviously analogous " to the horny knob which is present in the embryos of certain Birds but he doubted if it acted as a shell-breaker since he held that all the facts pointed to the " Oviviviparity " of the Monotremes. Later (1865), he recorded its existence also in the young of Echidna. W. K. Parker (1885) refers to its presence in a young Platypus, as did J. T. Wilson in 1894 and W. N. Parker in the same year, in the young Echidna. In a preliminary paper published in 1900, Wilson showed that the caruncle of the Monotreme is provided with a skeletal support of its own, in the form of a small bony nodule which he termed the os carunculæ. In his full paper (1902), he expressed the belief that it is formed by the fusion of thin trabeculae which are prolonged dorsally from the inferior lamellae (ventral laminae) of the premaxillae, but in the explanation of his fig. 3, pl. 37, the trabeculae in question are described as being connected with the ventral laminae of the bodies of the premaxillae as well as with the palatine processes of these bones. These latter represent the medial laminae of the premaxillae and the former, the lateral laminae described by Green (1930) and ourselves. We have shown that the lateral laminae at their anterior extremities merge into the medial and that the latter are then continued dorsally as the ascending processes. Green (1930) and de Beer and Fell (1936) have also assumed that the caruncular nodule is simply formed by the fusion in the middle line of the dorsal extremities of these processes. Our own observations, however, have led us to question the correctness of that assumption and to conclude that the os is an independent membranous ossification which has arisen in adaptation to the need of reinforcing the impact of the caruncular projection on the hard shell and with which the ascending processes of the premaxillae have only secondarily fused. We have suggested that they serve as struts for the support of the bone.

In support of this view there is the further fact that in the Marsupial *Caluromys philander*, Denison and Terry (1921) found the os carunculæ ossified as a median nodule of bone, although no ascending processes of the premaxillae were ossified at all.

The distribution and condition of the ascending processes of the premaxillae in the various groups of Sauropsida are of great interest from the point of view of the possible correlation between their presence and that of the egg-tooth on the one hand and the caruncle on the other.

In Lacertilia and Ophidia at the time of hatching, the ascending processes of the premaxillae are present; they are large and fused together. These are also the groups in which the egg-tooth is present.

In *Sphenodon* and in Birds the ascending processes of the premaxillae are present but not so large, and they remain unfused with one another. In Crocodilia and Chelonia, there are no ascending processes of the premaxillae. These are the groups which do not possess an egg-tooth, but are provided with a caruncle. It would seem, therefore, that the presence in the Squamata, of large, precociously formed, ascending processes of the premaxillae, fused together in the midline, is associated with the presence of an egg-tooth and not with that of a caruncle as we should have expected.

The Reptilian and Avian caruncle differs from that of the Monotreme in being a purely epidermal formation. Its occurrence, structure and development have



been described by, amongst others, Gardiner (1885), Röse (1892), Sluiter (1893), Voeltzkow (1899, 1903), Branca (1907), Rosenstadt (1912) and de Beer (1950). As is known, it takes the form of a low conical or knob-like projection of horn-like consistency which terminates in a more or less pointed apex and is situated in the mid-line on the dorsum of the snout shortly behind its tip. In the Crocodile, it is more flattened and terminates in two sharp points, an exceptional condition, due to the fact that it arises through the fusion of two large lateral papillae with a small median one (Voeltzkow, 1899, Sluiter, 1893). Structurally it consists of a dense, hard mass of horny material, formed from densely keratinized cells, resting on, and continuous with the Malpighian layer of the epidermis. It is invested superficially by an epitrichial layer of cells (very thick in the Reptiles, much thinner over its apex in the Chick) which is eventually cast off.

In the Monotreme, on the other hand, the caruncle as we have seen, is formed by a massive cone-shaped projection of the mesoderm, clothed by the epidermis which is only moderately thickened but whose superficial layers are strongly keratinized. Internally it is supported by the nodular os carunculæ and the ascending processes of the premaxillæ.

Such striking structural differences between the Sauropsidan and Monotreme caruncles might be held to indicate that they are merely analogous and not homologous structures which have arisen quite independently through parallelism in evolution, the outcome of the same functional need. Even if, as we have tried to show, the egg-teeth are homologous in the two groups, it does not necessarily follow that the caruncles in the two are genetically related. We have then these two alternatives before us: (a) to regard the caruncles of the Reptiles and Monotremes as genetically related, or (b) to regard them as analogous formations, the result of developmental parallelism. In support of the first alternative, some such consideration as the following might be urged. When the ancestral cold-blooded Reptile gave origin to the primitive warm-blooded Mammal, one of the outstanding changes effected was the transformation of the hard, scale-covered skin of the one into the soft, hair-clad skin of the other. May it not therefore be that the preponderance of the mesoderm and the reduction in the rôle of the ectoderm in the Monotreme caruncle are to be correlated with the much greater development of the dermis in the Mammal as compared with the Reptile, as well as with the, in general, greatly reduced potentiality of the epidermis of the Mammal for keratinization as compared with that of the Reptile? We have only to contrast the densely keratinized covering of the snout of the Reptile and the beak of the Bird with the relatively soft skin covering the snout of the Monotreme and to recollect that the limiting factor which conditions that difference relates to the ectoderm of the embryo, to see how it might have come about that a purely epidermal caruncle developed in the Reptile, and how it happened that the primitive Prototherian in forming its caruncle substituted a mesodermal core, supported by a bony nodule and with only a relatively thin epidermal covering, for the dense and hard purely epidermal caruncle of its ancestor.

We would suggest accordingly that the Monotreme caruncle is not an entirely new formation but has been evolved by a process of substitution from that of the Reptile, and is to be regarded as genetically related to it. In other words we

would regard the Monotreme caruncle as, to use Lankester's term (1877), homogenous with (*i.e.* "derived from one and the same ancestral source" as) that of the Reptile.

If on the other hand, the alternative view is regarded as the more probable, *viz.*, that the Monotreme caruncle is a structure *sui generis* and quite unrelated to that of the Reptile, the following implications would seem to arise:

(a) That the ancestral Monotreme had at one time a thin egg-shell, similar to that of existing oviparous Squamata which could be ripped open by the egg-tooth, and that a caruncle was absent.

(b) That later, as the egg became reduced in size owing to the gradual reduction in the amount of its contained yolk, it was retained for a longer period in the oviduct in order that that loss might be compensated for by absorption of the nutritive secretion of the oviducal glands. As a secondary result of that longer stay in the oviduct, it may be supposed that the shell gradually thickened and that as an adaptation to such a condition there followed the appearance of a shell-breaker of the type seen in existing Monotremes, as an entirely new formation.

Against this point of view, it may be argued that, whilst there is nothing inherently improbable in the conversion of a thin membranous shell into a thick calcified one, no recorded case of such a happening appears to be known. On the other hand, it should be remembered that no other group affords a precise parallel to the conditions obtaining in the Monotremes and that, consequently, negative evidence in this case is of little value.

The problem before us is not an easy one on which to reach a decision, but we express our preference for the first alternative.

#### BIBLIOGRAPHY.

- ALDROVANDUS, U. (1597). *Ornithologia*, Bonn.
- de BEER, G. R., & FELL, W. A. (1936). The development of the Monotremata.—Part III. The development of the skull of Ornithorhynchus. *Trans. zool. Soc. Lond.*, **23**, 1-28.
- de BEER, G. R. (1938). Embryology and Evolution. In "*Evolution: Essays presented to E. S. Goodrich*," Oxford, 57-78.
- de BEER, G. R. (1950). Caruncles and egg-teeth. *Proc. Linn. Soc. Lond.* **161**, 218-224.
- BOLK, L. (1912). On the structure of the dental system of reptiles. *Proc. Kon. Akad. Weten. Amst.*, **1912**, 950-961.
- BRANCA, A. (1907). Le diamant du Poulet. *C. R. Assoc. Anat., Lille*, **1907**, 81-87.
- BROOM, R. (1909). Observations on the development of the marsupial skull. *Proc. Linn. Soc. N.S.W.*, **34**, 195-214.
- BURRELL, H. (1927). *The Platypus*. Sydney. Angus & Robertson.
- BUTLER, P. M. (1937). Studies of the mammalian dentition. 1. The teeth of *Centetes ecaudatus* and its allies. *Proc. zool. Soc. Lond.*, B., **107**, 103-132.
- BUTLER, P. M. (1939). Studies of the mammalian dentition—differentiation of the post-canine dentition. *Proc. zool. Soc. Lond.*, B., **109**, 1-36.
- DENISON, W., & TERRY, R. J. (1921). The chondrocranium of *Caluromys*. *Washington Univ. Stud.*, **8**, 161-182.
- GARDINER, E. G. (1885). Beiträge zur Kenntniss des Epitrichiums und der Bildung des Vogelschnabels. *Arch. mikr. Anat.*, **24**, 289-338.
- GOLDSTEIN, H. (1890). Beiträge zur Kenntnis des Eizahnes bei den Reptilien. Inaug. Diss. Königsberg i. Pr.



- GREEN, H. L. (1930). A description of the egg-tooth of *Ornithorhynchus*, together with some notes on the development of the palatine processes of the premaxillae. *J. Anat. Lond.*, **64**, 512-522.
- GREEN, H. L. H. H. (1937). The development and morphology of the teeth of *Ornithorhynchus*. *Philos. Trans.*, **228**, 367-420.
- HAACKE, W. (1885). Über eine neue Art uterinaler Brutpflege bei Reptilien. *Zool. Anz.*, **8**, 435-439.
- HARRISON, H. S. (1901). The development and succession of teeth in *Hatteria punctata*. *Quart. J. micr. Sci.*, **44**, 161-213.
- HARRISON, H. S. (1901). *Hatteria punctata*, its dentition and its incubation period. *Anat. Anz.*, **20**, 145-158.
- HILL, J. P. (1910). The early development of the Marsupialia, with special reference to the native cat (*Dasyurus viverrinus*). *Quart. J. micr. Sci.*, **56**, 1-134.
- HUNTER, JOHN, v. Hunterian MS. in *Descriptive and Illustrated Catalogue of the Museum of the Royal College of Surgeons in London*. London, 1840, vol. **5**, 31; pl. 76, figs. 17-18; and *The Scientific Works of John Hunter*, edited by Prof. Owen, **1**, 216. London, 1861.
- KEIBEL, F. (1912). Wie zerbricht der ausschöpfende Vogel die Eischale? *Anat. Anz.*, **41**, 381-382.
- LANKESTER, E. RAY (1877). *Notes on Embryology and Classification*. London. J. & A. Churchill.
- LECHE, W. (1893). Über die Zahnentwicklung von *Iguana tuberculata*. *Anat. anz.*, **8**, 793-800.
- MATTHEW, W. D. (1916). A Marsupial of the Belly River Cretaceous. *Bull. Amer. Mus. nat. Hist.*, **35**, 477-500.
- MCCOY, F. (1885). *Trachydosaurus rugosus* (Gray). *Prodromus of the Zoology of Victoria*, **2**, Decade XI, 3-5, pl. 102.
- OWEN, R. (1835). On the young of *Ornithorhynchus paradoxus* (Blum.) *Trans. zool. Soc. Lond.*, **1**, 221-228.
- OWEN, R. (1865). On the marsupial pouches, mammary glands and mammary foetus of *Echidna hystrix*. *Philos. Trans.*, **155**, 671-686.
- PARKER, W. K. (1885). *On Mammalian Descent*. London: C. Griffin & Co., 1885.
- PARKER, W. N. (1894). On some points in the structure of the young of *Echidna aculeata*. *Proc. zool. Soc. Lond.*, **1894**, 3-14.
- RÖSE, C. (1892). Über die Zahnleiste und die Eischwiele der Sauropsiden. *Anat. Anz.*, **7**, 748-758.
- RÖSE, C. (1893). Über die Zahnentwicklung der Crocodile. *Morph. Arb.*, **3**, 195-228.
- RÖSE, C. (1894). Über die Zahnentwicklung der Kreuzotter. *Anat. Anz.*, **9**, 439-451.
- ROSENSTADT, R. (1912). Untersuchungen über die Histogenese des Eizahnes und des Schnabels beim Hühnchen. *Arch. mikr. Anat.*, **79**, 612-636.
- SEMON, R. (1894). Zur Entwicklungsgeschichte der Monotremen. *Zoologische Forschungsreisen in Australien, etc.*, **2**, 59-74. *Denkschr. med. naturw. Ges. Jena*, **5**, 59-74.
- SEYDEL, O. (1899). Der Eizahn von *Echidna*, seine Entwicklung und sein Bau. In Semon, *Zoologische Forschungsreisen in Australien, etc.*, **3**, 519-529. *Denkschr. med. naturw. Ges. Jena*, **6**, 519-529.
- SIMPSON, G. G. (1928). *A Catalogue of the Mesozoic Mammalia*. British Museum (N. H.) London, 1928.
- SLUITER, C. Ph. (1893). Über den Eizahn und die Eischwiele einiger Reptilien. *Morph. Jb.*, **20**, 75-89.
- VOELTZKOW, A. (1899). Biologie und Entwicklung der äusseren Körperform von *Crocodilus madagascariensis*, Grand. *Abh. senckenb. Ges.*, **26**, 5-149.
- VOELTZKOW, A. (1903). Gesichtsbildung und Entwicklung der äusseren Körperform bei *Chelone imbricata*, Schweigg. *Abh. senckenb. Ges.*, **27**, 181-190.
- WEINLAND, D. F. (1856). Ueber den Eizahn der Ringelnatter. *Jh. Ver. vaterl. Naturk. Württemb.*, **12**, 90-93.
- WILSON, J. T. (1894). Description (with figures) of a young specimen of *Ornithorhynchus anatinus* from the collection of the Australian Museum, Sydney. *Proc. Linn. Soc. N.S.W.* (Ser. 2), **9**, 682-690.
- WILSON, J. T. (1900). On the skeleton of the snout and os carunculae of the mammary foetus of the Monotremes. *Proc. Linn. Soc. N.S.W.*, **25**, 58-59.
- WILSON, J. T. (1901). On the skeleton of the snout of the mammary foetus of the Monotremes. *Proc. Linn. Soc. N.S.W.*, **26**, 717-737.

- WILSON, J. T., & HILL, J. P. (1907). Observations on tooth development in *Ornithorhynchus*. *Quart. J. Micr. Sci.*, **51**, 137-165.
- WOERDEMAN, M. W. (1919). Beiträge zur Entwicklungsgeschichte von Zähnen und Gebiss der Reptilien. 1-111. *Arch. mikr. Anat.*, **92**, 105-244.
- YARRELL, W. (1826). On the small horny appendage to the upper mandible in very young chickens. *Zool. Journ.*, **2**, 433-437.



## EXPLANATION OF PLATES.

## PLATE I.

- Fig. 1.—Platypus K. Median sagittal section (5-2-6) showing the egg-tooth (*e.th.*) and caruncle (*car.*). ( $\times 75$ .)
- Fig. 2.—Platypus K. Sagittal section (5-2-6) to show details of egg-tooth. ( $\times 136$ .)
- Fig. 3.—Platypus KK. Transverse section (5-2-13) of egg-tooth, showing commencing differentiation of the enamel organ. *b.fd.* basal fold, *b.gr.* basal groove, *e.ep.* enamel epithelium. ( $\times 180$ .)
- Fig. 4.—Platypus KK. Transverse section (9-1-13), showing the basal region of the egg-tooth, on one side. *b.ep.* buccal epithelium, *b.fd.* basal fold, *b.gr.* basal groove, *b.m.* basement membrane, *e.ep.* enamel epithelium, *od.* odontoblast layer, differentiating. ( $\times 278$ .)
- Fig. 5.—Platypus L. Transverse section (6-3-10), showing the egg-tooth and caruncle. *c.os.c.* mesenchymal condensation in site of os carunculae, *en.o.* differentiating enamel organ, *m.c.* condensation for marginal cartilage, *m.px.p.* primordium of medial lamina of premaxilla, *md.c.* median "rostral" condensation. ( $\times 75$ .)

## PLATE II.

- Fig. 6.—Platypus L. Transverse section (7-3-10) of egg-tooth. *b.m.* basement membrane, *b.sp.* basal space, *e.ep.* enamel epithelium, *od.* odontoblast layer, *o.ep.* outer enamel epithelium, *s.r.* stellate reticulum. ( $\times 325$ .)
- Fig. 7.—Platypus V. Transverse section (5-2-12) through the egg-tooth. *at.b.* attaching bone trabeculae, *den.* dentine, *m.px.* trabeculae of medial lamina of premaxilla, *r.v.* "rostral" vessel. ( $\times 225$ .)
- Fig. 8.—Platypus V. Transverse section (3-2-12) showing base of egg-tooth. Note continuity between attaching bone trabeculae (*at.b.*) and dentine (*den.*). ( $\times 290$ .)
- Fig. 9.—Platypus VV. Transverse section (5-4-8), passing through the caruncle (*car.*) and the egg-tooth. *m.px.* medial lamina of premaxilla. ( $\times 88$ .)

## PLATE III.

- Fig. 10.—Platypus VV. Transverse section (4-4-8) through the egg-tooth, showing the forming medial lamina (*m.px.*) and the ascending process (*a.px.*) of the premaxilla. ( $\times 184$ .)
- Fig. 11.—Platypus VV. Transverse section (7-3-8) through the egg-tooth, 0.18 mm. behind fig. 10, showing the medial (*m.px.*) and the lateral (*l.px.*) laminae of the premaxillae and the attaching bone (*at.b.*). ( $\times 184$ .)
- Fig. 12.—Platypus VV. Transverse section (10-3-8) to show the finer structure of the egg-tooth. Note the continuity of the dentine with the attaching bone trabeculae (*at.b.*) and also with the basement membrane (*b.m.*). ( $\times 368$ .)

Fig. 13.—Platypus VV. Transverse section (4-4-8) through the base of the egg-tooth, showing the odontoblasts (*od.*), dentine (*den.*) enamel epithelium (*e.ep.*), stratum intermedium (*st.i.*) and stellate reticulum cells (*s.r.*). ( $\times 517$ .)

## PLATE IV.

Fig. 14.—Platypus VV. Transverse section (7-4-8) showing the upper portion of the median "rostral" condensation (*md.c.*) with the primordia of the trabeculae of the ascending premaxillary processes (*a.px.t.*), and its continuity with the caruncular bone condensation (*c.os.c.*). ( $\times 270$ .)

Fig. 15.—Platypus GW.1. Transverse section (6-3-5) through the egg-tooth. Note the vascularity of the dentinal pulp. ( $\times 210$ .)

Fig. 16.—Platypus GW.2. Transverse section (6-3-1) through the egg-tooth. The trabeculae of the medial premaxillary laminae (*m.px.*) and of the attaching bone (*at.b.*) are in course of formation. *den.* dentine, *od.* layer of odontoblasts. ( $\times 210$ .)

Fig. 17.—Platypus GW.3. Transverse section (1-5-2) through the egg-tooth, showing the enamel organ, now fully formed, the well-marked layer of dentine (*den.*), the attaching bone trabeculae (*at.b.*) and the primordia of the medial (*m.px.*) and the lateral (*l.px.*) laminae of the premaxillae. *r.v.* "rostral" vessel. ( $\times 228$ .)

## PLATE V.

Fig. 18.—Platypus GW.3. Transverse section (2-2-3) through the root of the egg-tooth, showing the attaching bone (*at.b.*) the extensive lateral laminae of the premaxillae (*l.px.*) and the medial laminae (*m.px.*) of the same. ( $\times 175$ .)

Fig. 19.—Platypus GW.3. Transverse section (4-1-2) through the ascending processes of the premaxillae (*a.px.*). *car.v.* caruncular vessel. ( $\times 225$ .)

Fig. 20.—Platypus GW.3. Transverse section (1-5-1), showing the junction of the fused ascending premaxillary processes (*a.px.*), with the base of the caruncular bone (*os.c.*). ( $\times 278$ .)

Fig. 21.—GW.3. Transverse section (2-4-1) through the caruncle, to show the os carunculæ (*os.c.*) and the caruncular epidermis (*ep.c.*).

Fig. 22.—GW.3. Transverse section (2-4-1) through the os carunculæ to show its minute structure. Note the osteoblasts (*ost.*) forming a layer on the upper side of the figure, below them, osteoblasts in groups (*ost.gr.*) separated by fine lines of matrix and lower still, lacunae (*lac.*) separated by strands of matrix (*m.*) and containing osteoblasts, variously arranged. ( $\times 675$ .)



## PLATE VI.

- Fig. 23.—Echidna, EBB. Transverse section (5-3-1), showing the egg-tooth, surrounded by the remains of the enamel organ (*r.eo.*) and the downward reflection of the oral epithelium (*b.ep.*), the attaching bone (*at.b.*) continuous with the medial laminae of the premaxillae (*m.px.*), the rostral cartilage (*r.c.*) and the os carunculae (*os.c.*). ( $\times 92$ .)
- Fig. 24.—Echidna, EBB. Transverse section (2-4-1), 0.08 mm. behind fig. 23, passing through the root of the egg-tooth, showing the dentinal pulp (*d.p.*) enclosed ventrally and laterally by attaching bone (*at.b.*), and the medial (*m.px.*) and the lateral (*l.px.*) laminae of the premaxillae. ( $\times 135$ .)
- Fig. 25.—Echidna, EBB. Transverse section (8-2-1), showing the ascending processes (*a.px.*) passing up from the medial laminae of the premaxillae, between, and in contact with the horns (*r.c.*) of the rostral cartilage. ( $\times 140$ .)
- Fig. 26.—Echidna, EBB. Transverse section (10-2-1), 0.02 mm. behind fig. 25, to show the continuity of the ascending processes (*a.px.*) with the cranial extremity of the os carunculae (*os.c.*). *d.l.* presumed dental lamina. ( $\times 150$ .)

## PLATE VII.

- Figs. 29 to 34.—Platypus WW. Series of six transverse sections through the snout, illustrating the structural relations of the egg-tooth and the carunculae to the bony skeleton. For description, see text, pp. 520-521. ( $\times 44$ .)

## PLATE VIII.

- Fig. 27.—Echidna, EBB. Transverse section (6-3-1), to show the os carunculae (*os.c.*). *r.c.* "rostral" cartilage. ( $\times 192$ .)
- Fig. 28.—Echidna, EBB. Transverse section (3-4-1) to show the structure of the caruncular epidermis. ( $\times 368$ .)
- Fig. 35.—Platypus WW. Transverse section (4-1-2) passing through the base of the egg-tooth and showing the attaching bone (*at.b.*) in process of resorption, the dentinal pulp (*d.p.*), the relatively thick dentinal layer (*den.*) and the remains of the enamel organ (*r.eo.*), enamel epithelium (*e.ep.*) and odontoblast layer (*od.*). ( $\times 225$ .)
- Fig. 36.—Platypus WW. Transverse section (6-1-2) through the base of the egg-tooth, specially to show the osteoclasts (*ocl.*) in the dentinal pulp and in relation to the attaching bone (*at.b.*). ( $\times 315$ .)
- Fig. 37.—Platypus WW. Transverse section (7-2-2) through the base of the egg-tooth, showing the structure of the "dentinal" layer. *p.den.* predentine, *den.* dentine, *en.* presumed enamel layer, *r.eo.* remains of enamel organ, *od.* remains of odontoblast layer, *ocl.* osteoclast. ( $\times 667$ .)

Fig. 38.—*Platypus* WW. Transverse section (3-2-2), showing the junction of the ascending processes of the premaxillae (*a.px.*) with the os carunculae (*os.c.*). ( $\times 180$ .)

Fig. 39.—*Platypus* WW. Transverse section (6-3-2) through the caruncle to show the structure of the os carunculae (*os.c.*). ( $\times 180$ .)

Fig. 40.—Transverse section (4-3-2) through the caruncle to show the structure of the epidermis. ( $\times 368$ .)

## PLATE IX.

Fig. 41.—*Echidna* EBB. Entire view of embryo, from the left side, seen lying on a portion of the shell. ( $\times$  about 4.5.)

Fig. 42.—*Platypus* X. Transverse section of the toothlet "*dv*" of the upper jaw, situated on the labial side of the dental lamina (*d.l.*), and showing its enamel organ indenting the buccal epithelium, its dentinal papilla and dentinal shell. (*cf.* Green (1937), pl. 34, fig. 28). ( $\times 265$ .)

Fig. 43.—Reproduction of fig. 32, Taf. VIII of Woerdeman (1919) showing in transverse section a toothlet from the lower jaw of an embryo of *Crocodylus porosus* (A, H.L. 12 mm.), for comparison with fig. 42.

Fig. 44.—*Trichosurus vulpecula*. 14 mm. G.L. Transverse section (1-4-1) through the snout showing the rudimentary dentinal papilla (*r.d.p.*) and its relations to the cartilages of the nasal capsules (*c.n.c.*) and the rudiments of the premaxillary bones (*r.prm.*). ( $\times 30$ .)

Fig. 45.—*Trichosurus vulpecula*. 13.5 mm. G.L. Transverse section (1-4-3) through the rudimentary dentinal papilla (*r.d.p.*), showing the condensation of mesenchyme cells forming it and its indentation of the buccal epithelium (*b.ep.*). ( $\times 125$ .)

Fig. 46.—*Trichosurus vulpecula*. 14 mm. G.L. Transverse section (1-3-12) through the rudimentary dentinal papilla (*r.d.p.*) showing the high degree of capillary (*cap.*) vascularization of the sub-epithelial mesenchyme. ( $\times 208$ .)

Fig. 47.—*Trichosurus vulpecula*. 15 mm. G.L. Transverse section (1-4-7) through the rudimentary dentinal papilla (*r.d.p.*) showing its relations to the premaxillary bones (*prm.*). ( $\times 200$ .)

## PLATE X.

Fig. 48.—*Phascolarctos cinereus*. 16.5 mm. G.L. Transverse section (1-4-5) through the rudimentary dentinal papilla (*r.d.p.*). ( $\times 96$ .)

Fig. 49.—*Phascolarctos cinereus*. 18 mm. G.L. Transverse section (2-1-1), showing the relations of the rudimentary dentinal papilla (*r.d.p.*) to the premaxillary bones (*prm.*) and to the attaching bone trabeculae (*at.b.*). ( $\times 120$ .)

Fig. 50.—*Didelphys aurita*. 8.5 mm. H.L. Transverse section (2-1-4) showing the connective tissue condensation representing the ascending processes of the premaxillae (*md.c.*). ( $\times 50$ .)



Fig. 51.—*Didelphys aurita*. 8.5 mm H.L. Transverse section (2-2-5) slightly posterior to that shown in fig. 50, showing the connective tissue condensation representing the os carunculæ (*c.os.c.*). ( $\times 50$ .)

Fig. 52.—*Caluromys philander*. 8.25 mm. H.L. Transverse section (1-4-6) showing the connective tissue condensation representing the ascending processes of the premaxillæ (*md.c.*). ( $\times 67$ .)

Fig. 53.—*Caluromys philander*, 8.25 mm. H.L. Transverse section (2-1-4) slightly posterior to that shown in fig. 52, showing the condensation of mesenchyme representing the os carunculæ (*c.os.c.*). ( $\times 67$ .)

#### LIST OF REFERENCE LETTERS.

<i>a.px.</i> ascending process, premaxilla.	<i>m.c.</i> marginal cartilage.
<i>at.b.</i> attaching bone trabeculae.	<i>m.px.</i> medial lamina, premaxilla.
<i>b.ep.</i> buccal epithelium.	<i>md.c.</i> median "rostral" condensation, site of <i>a.px.</i>
<i>b.fd.</i> basal fold.	<i>n.s.</i> nasal septum.
<i>b.gr.</i> basal groove.	<i>n.s.c.</i> condensation, nasal septum.
<i>b.m.</i> basement membrane.	<i>ocl.</i> osteoclast.
<i>b.sp.</i> basal (lymph) space.	<i>od.</i> layer of odontoblasts.
<i>c.os.c.</i> condensation in site of os carunculæ.	<i>os.c.</i> os carunculæ.
<i>c.n.c.</i> cartilage of nasal capsule.	<i>ost.</i> osteoblasts.
<i>cap.</i> capillary.	<i>o.ep.</i> outer enamel epithelium.
<i>car.</i> caruncle.	<i>p.den.</i> predentine.
<i>car.v.</i> median caruncular vessel.	<i>prm.</i> premaxillary bone.
<i>d.l.</i> dental lamina.	<i>r.c.</i> rostral cartilage.
<i>d.p.</i> mesodermal (dentinal) papilla.	<i>r.d.p.</i> rudimentary dentinal papilla.
<i>den.</i> dentine.	<i>r.eo.</i> remains of enamel organ.
<i>e.ep.</i> enamel epithelium.	<i>r.prm.</i> rudiment of premaxilla.
<i>en.</i> enamel.	<i>r.v.</i> "rostral" vessel.
<i>en.o.</i> enamel organ.	<i>s.e.m.</i> sub-epithelial mesenchyme.
<i>ep.c.</i> caruncular epidermis.	<i>s.r.</i> stellate reticulum.
<i>e.th.</i> egg-tooth.	<i>st.i.</i> stratum intermedium.
<i>l.j.</i> lower jaw.	
<i>l.px.</i> lateral lamina, premaxilla.	



Fig. 1

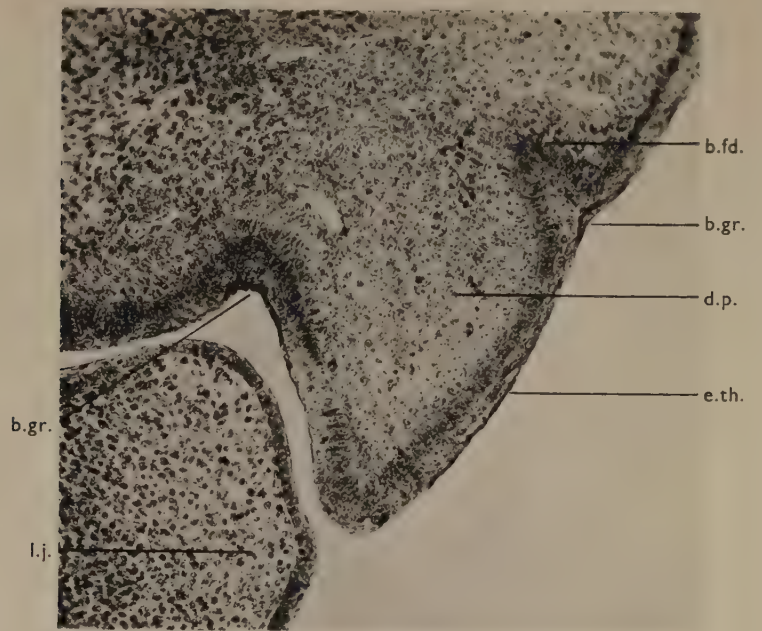


Fig. 2

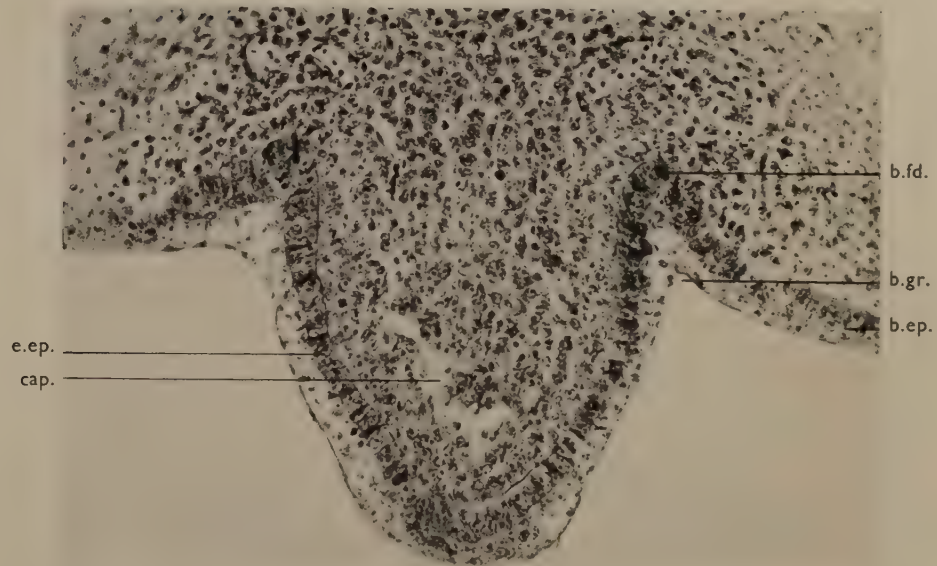


Fig. 3

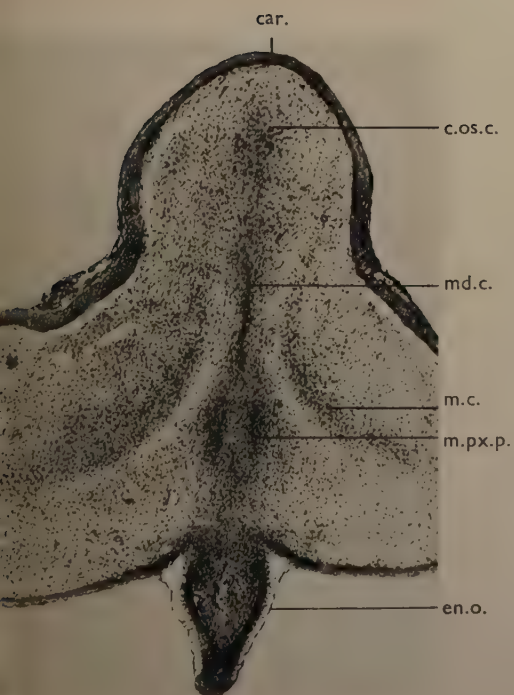


Fig. 5

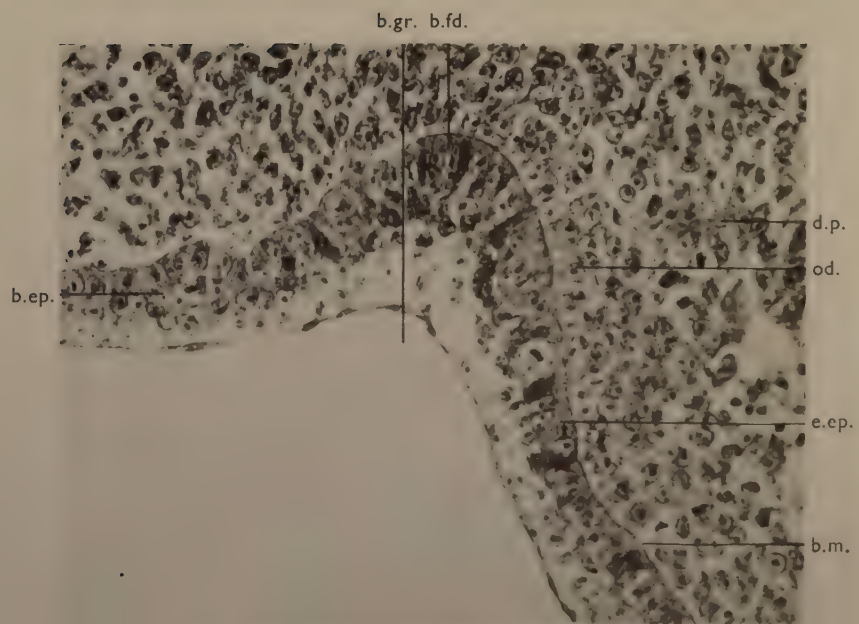








Fig. 6

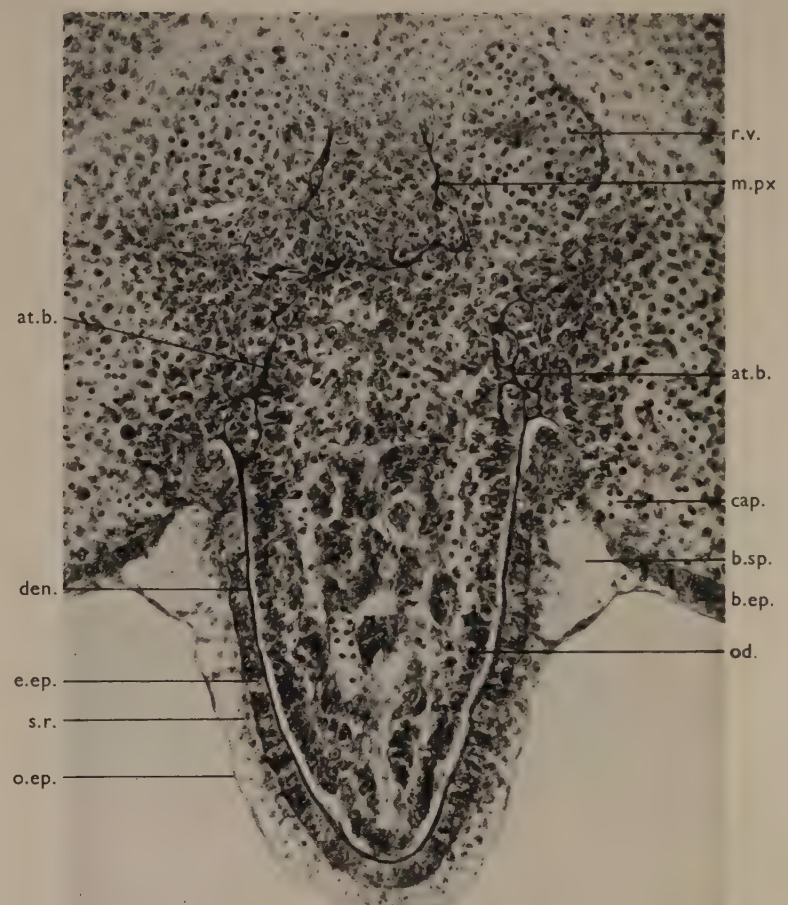


Fig. 7

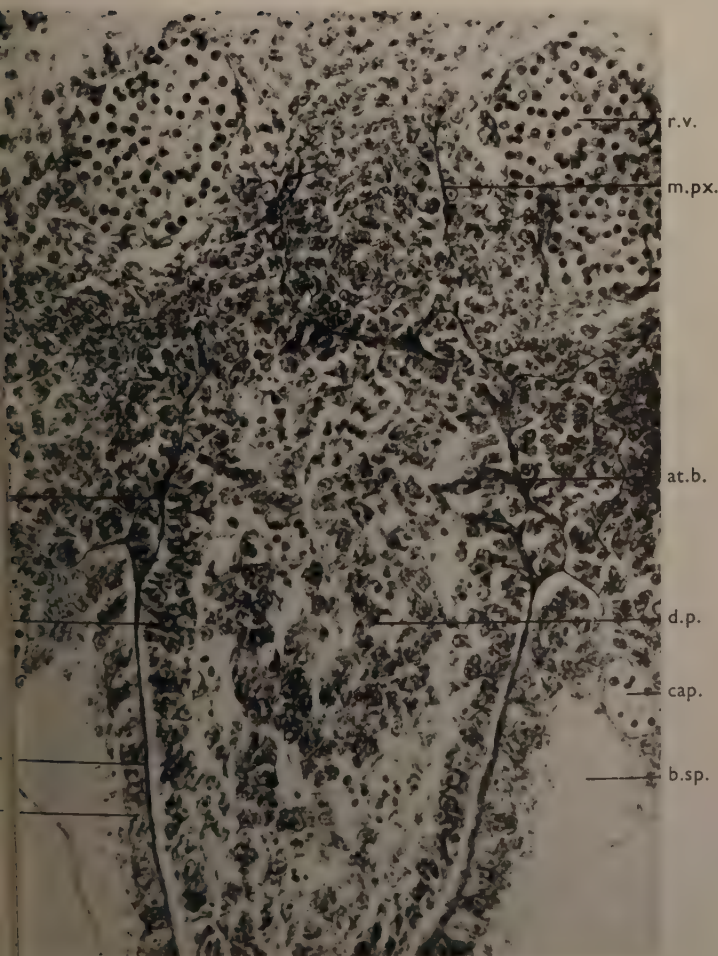


Fig. 8

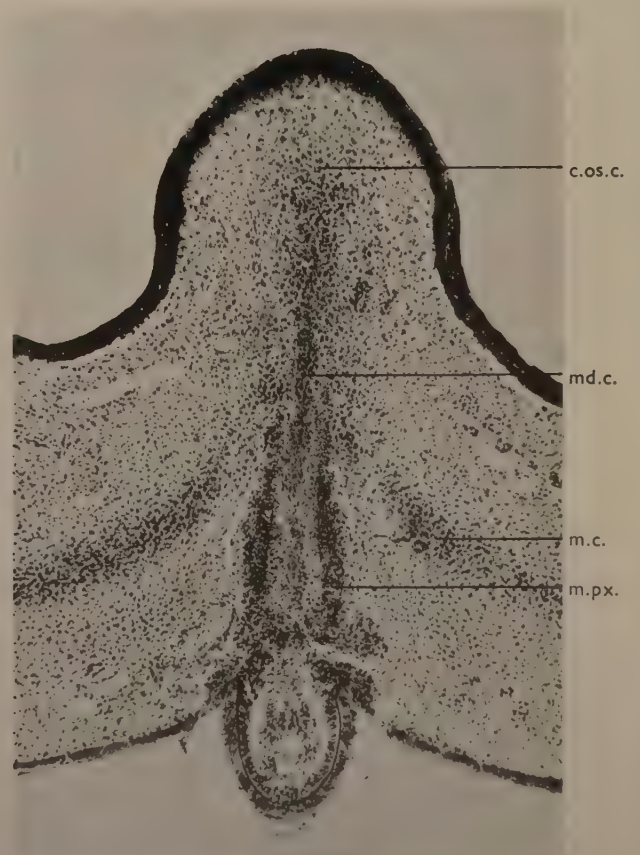


Fig. 9





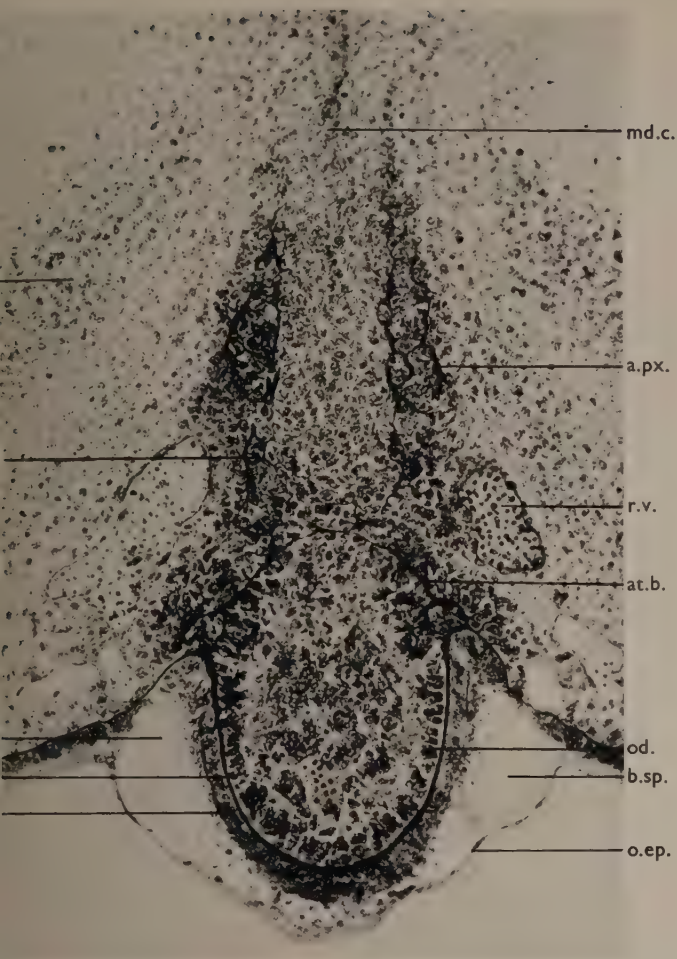


Fig. 10

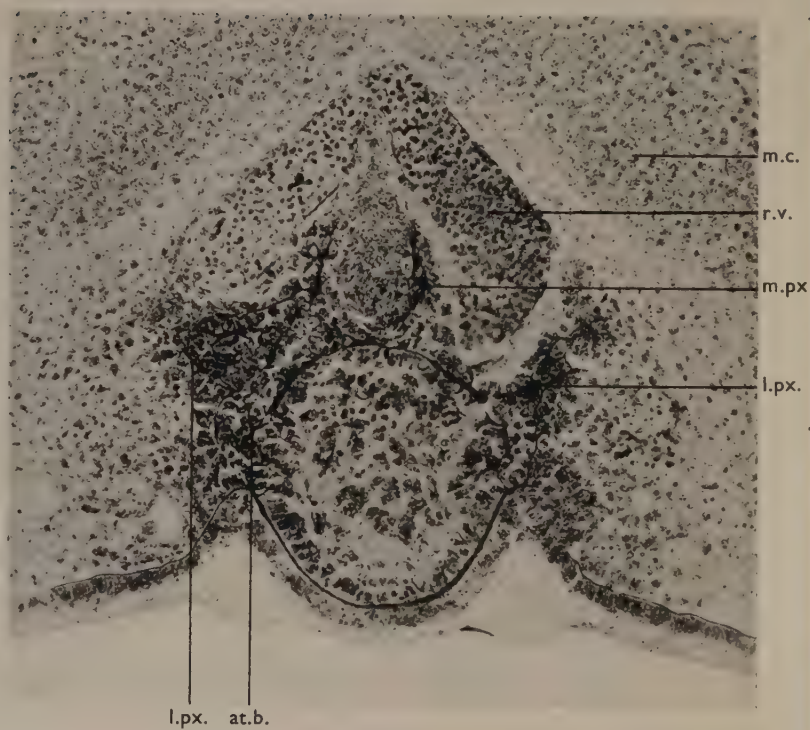


Fig. 11



Fig. 12

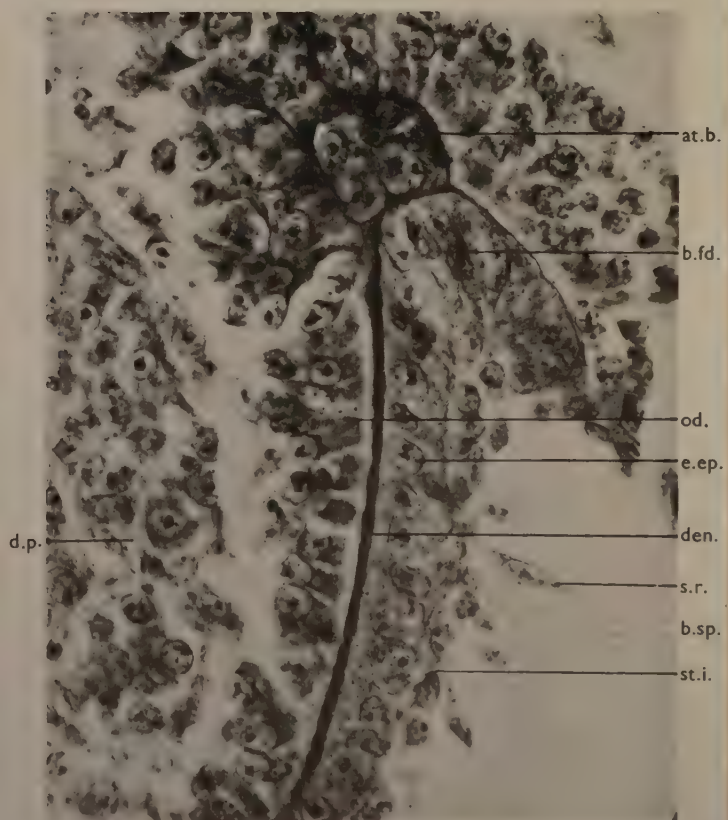


Fig. 13





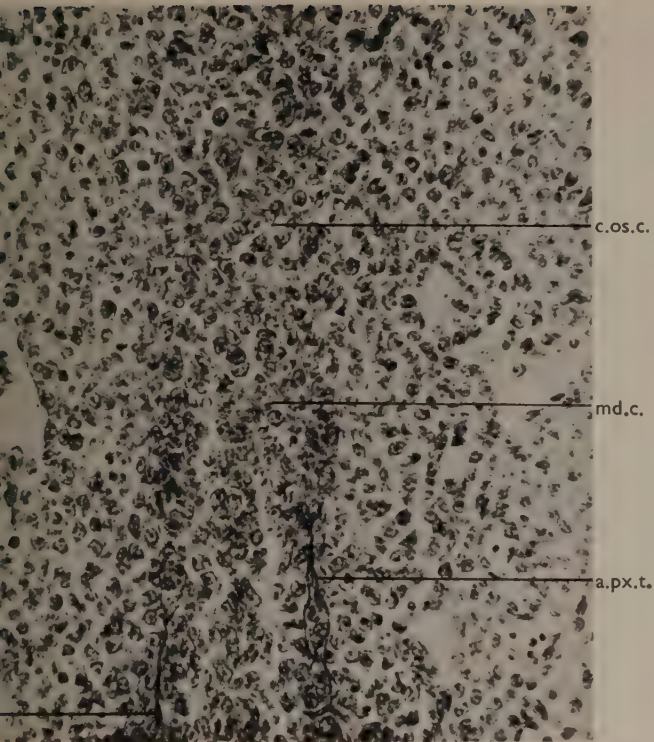


Fig. 14



Fig. 15

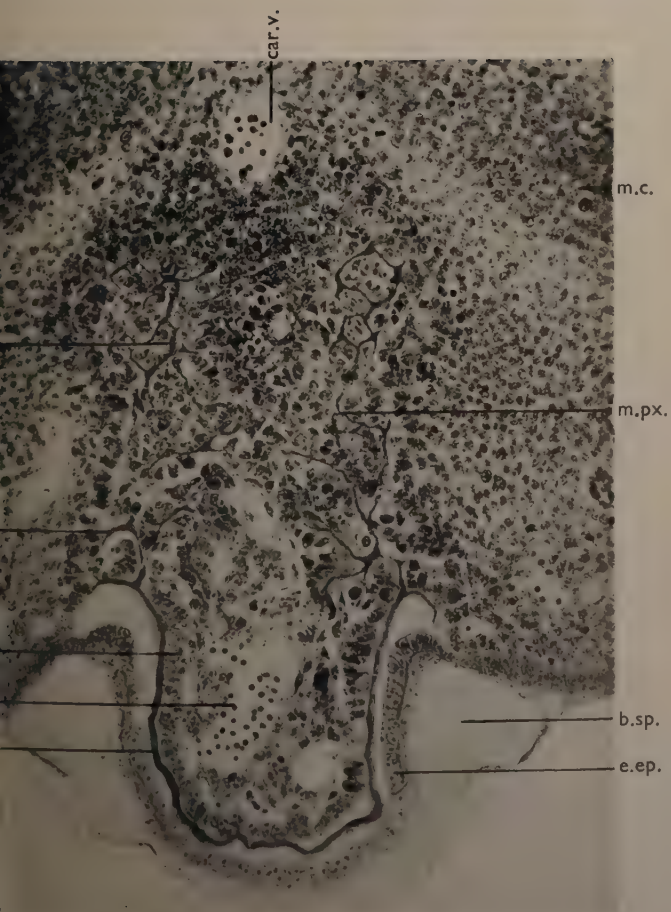


Fig. 16

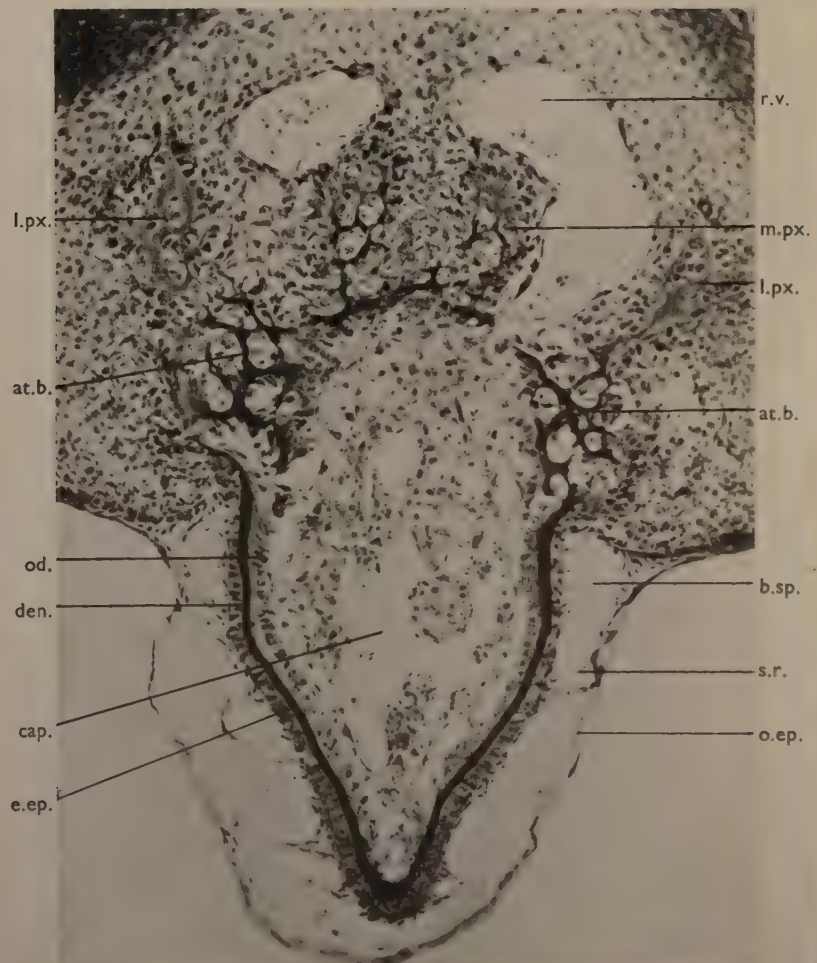


Fig. 17





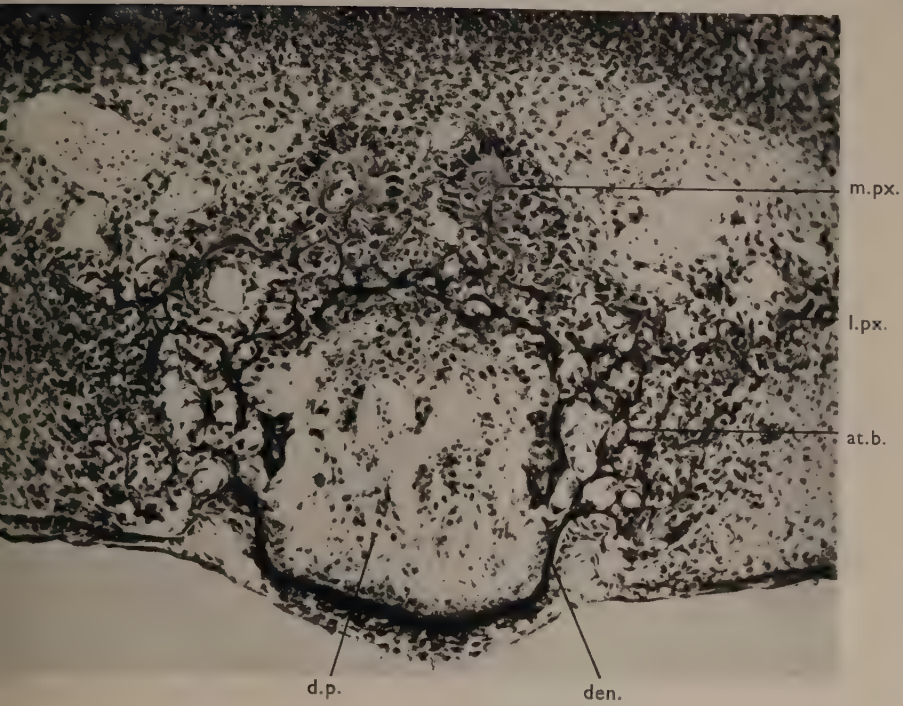


Fig. 18

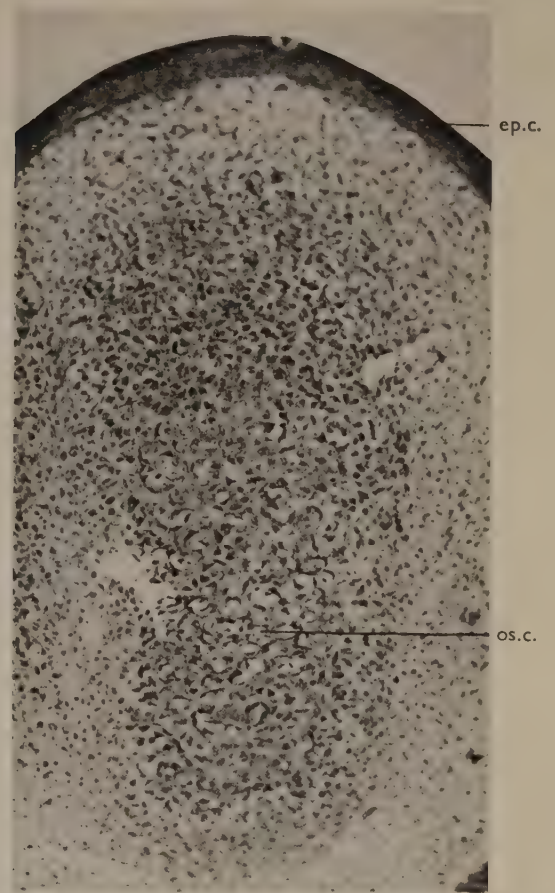


Fig. 21

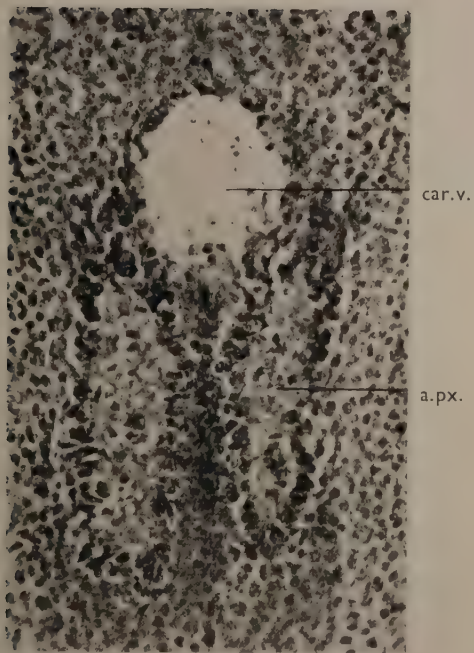


Fig. 19



Fig. 20

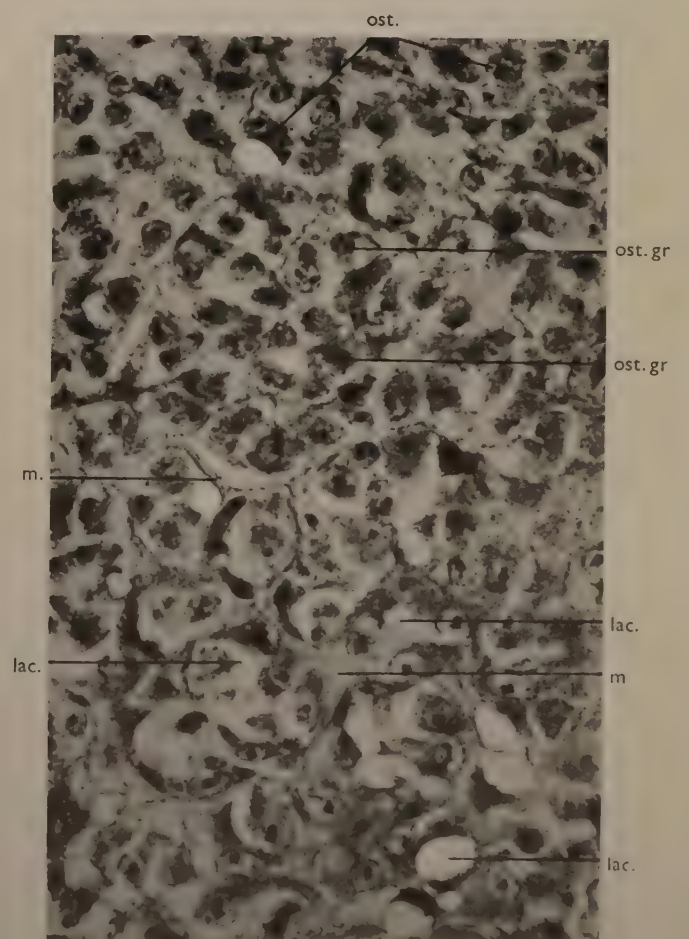


Fig. 22





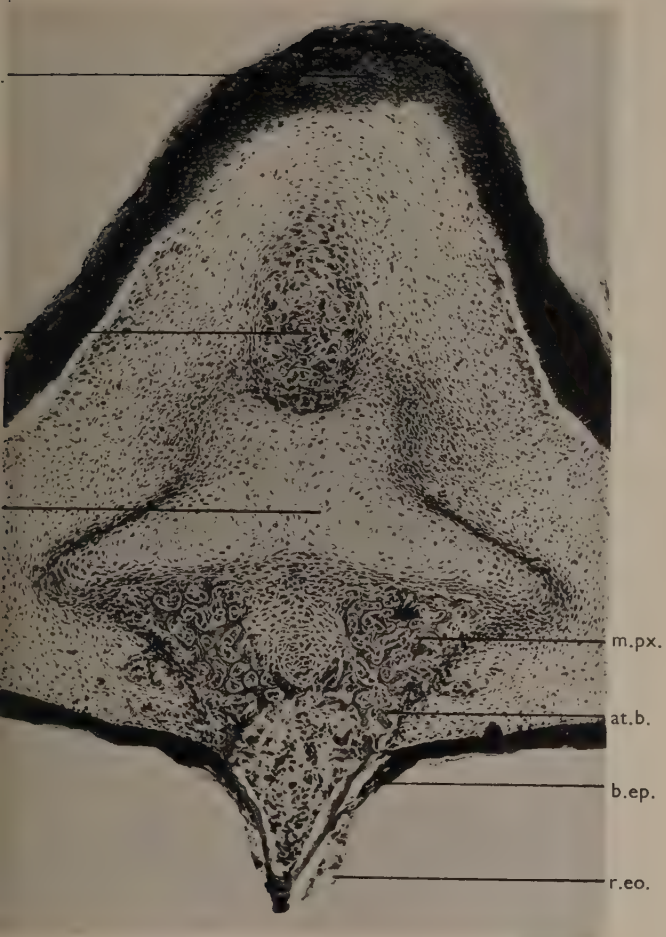


Fig. 23



Fig. 26

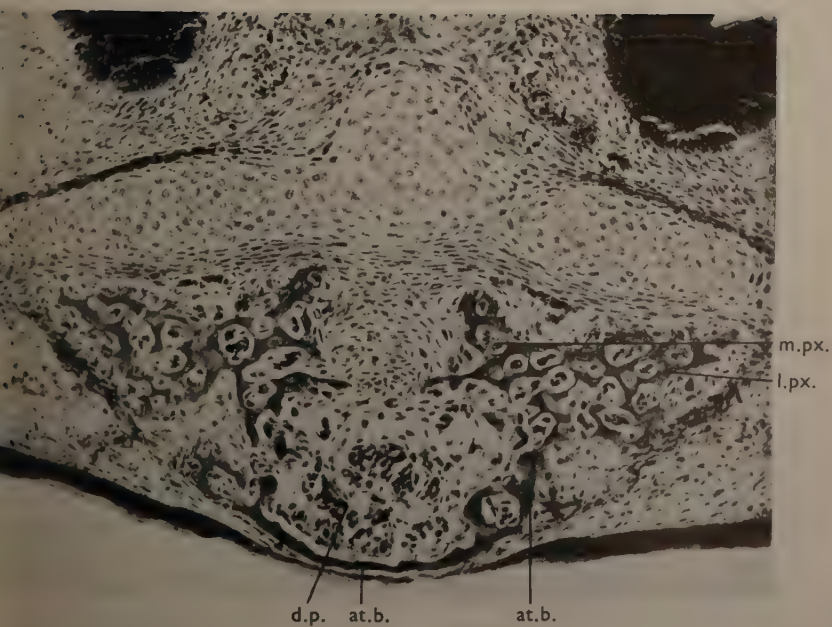


Fig. 24

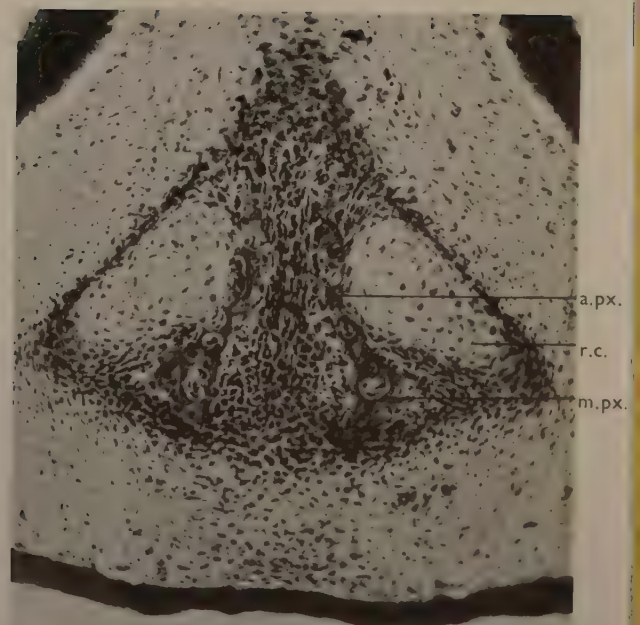


Fig. 25





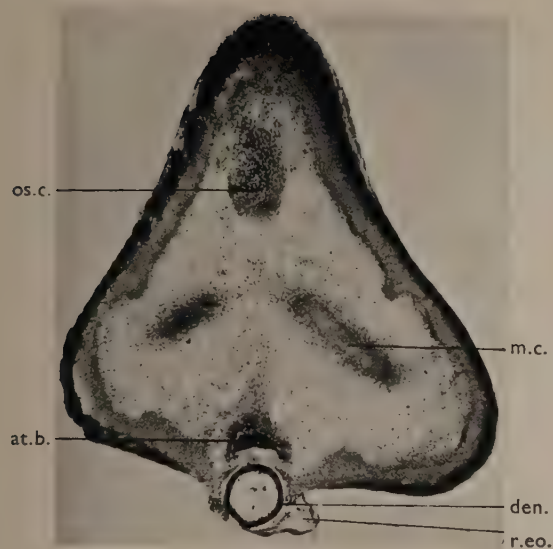


Fig. 29

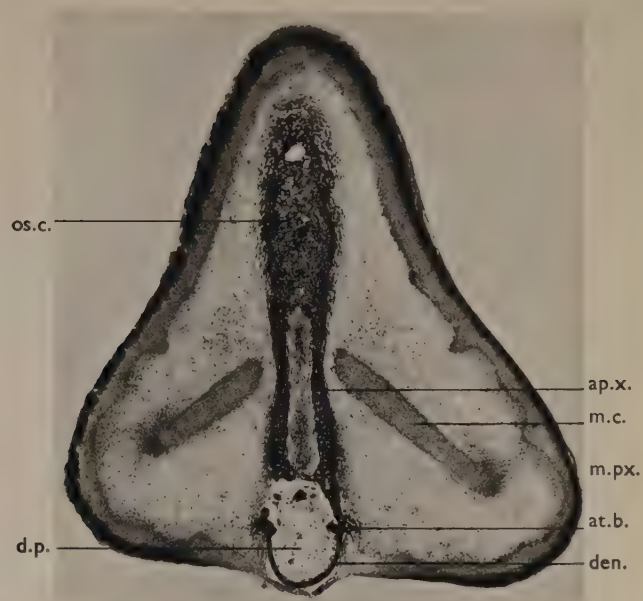


Fig. 30

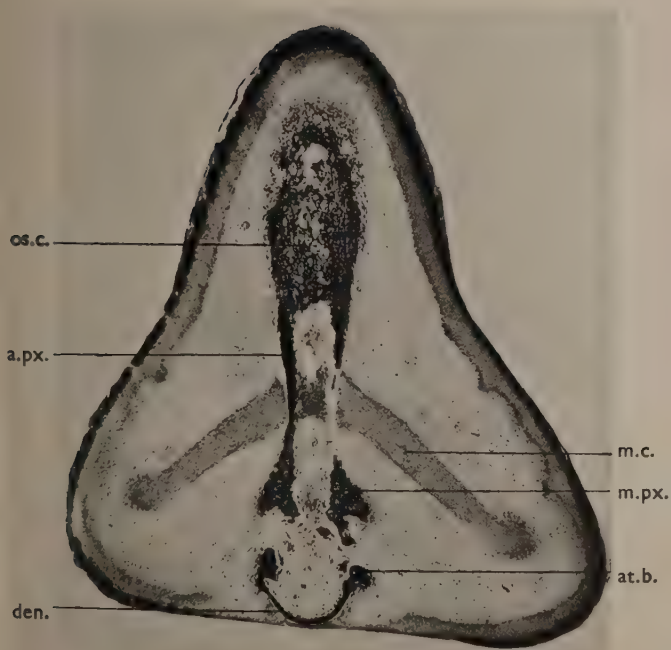


Fig. 31

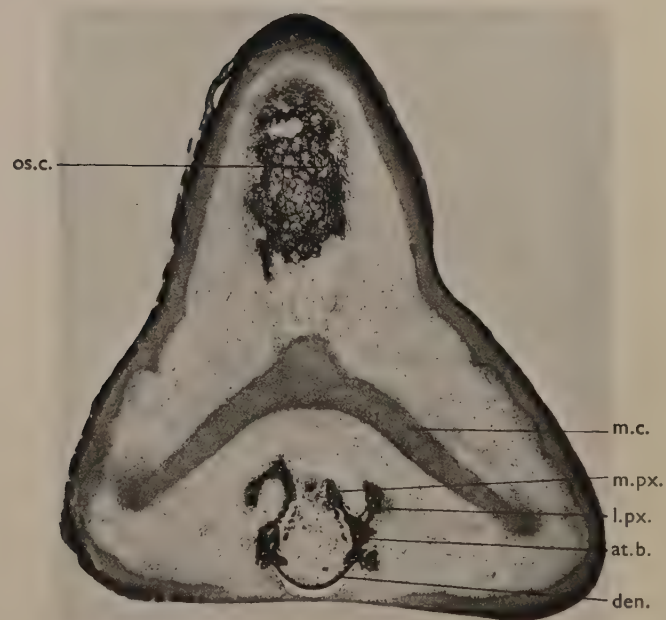


Fig. 32

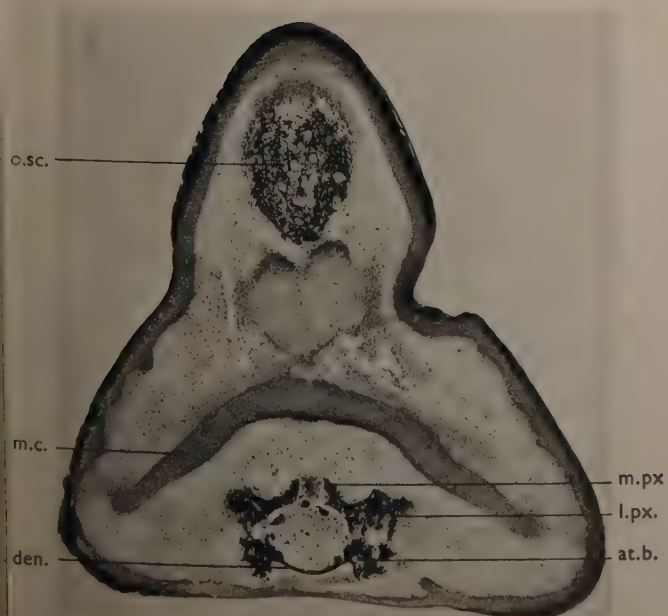








Fig. 27

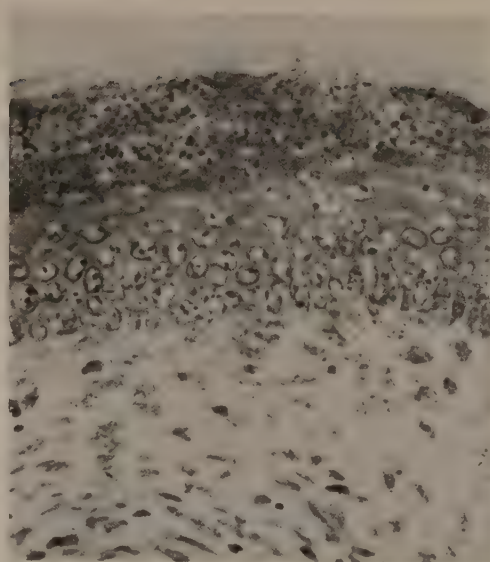


Fig. 28



Fig. 40



Fig. 35



Fig. 39



Fig. 38

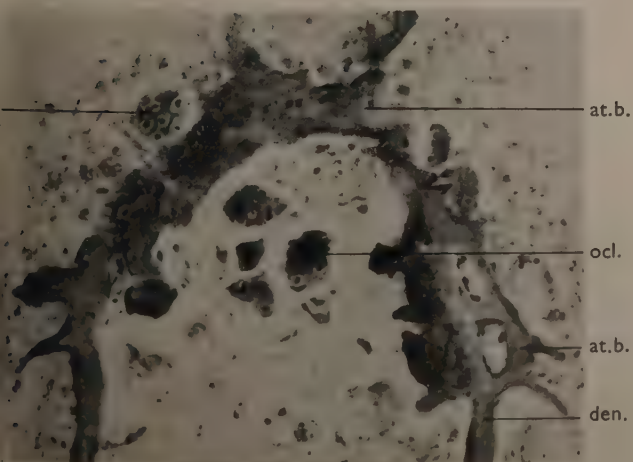


Fig. 36

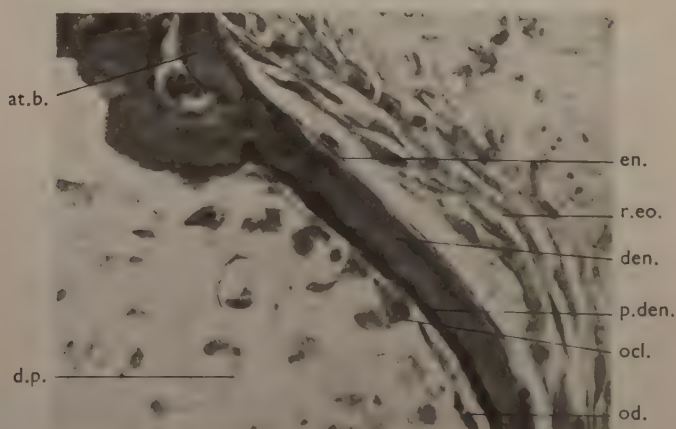


Fig. 37







Fig. 41

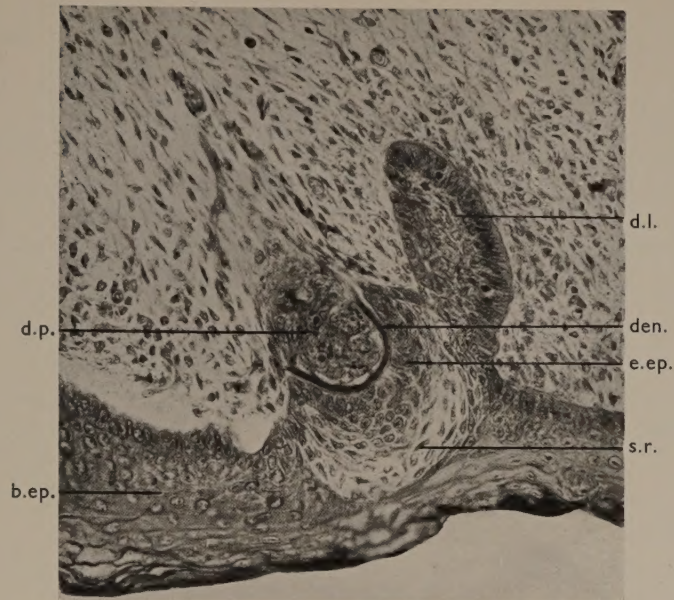


Fig. 42

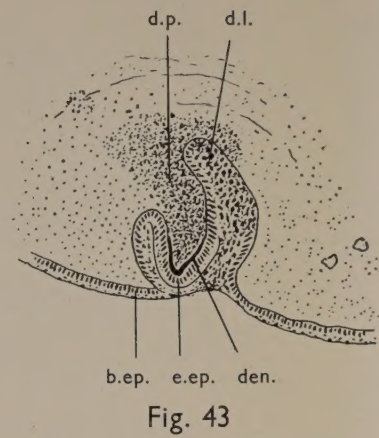


Fig. 43

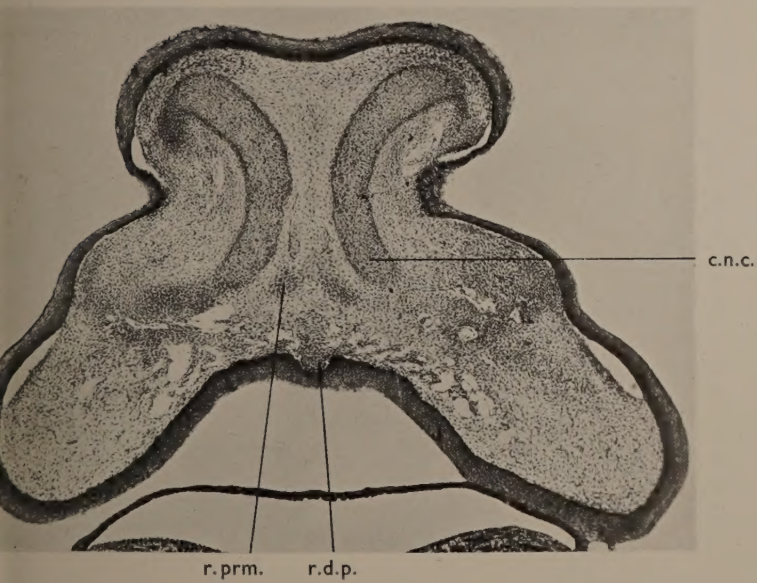


Fig. 44



Fig. 45

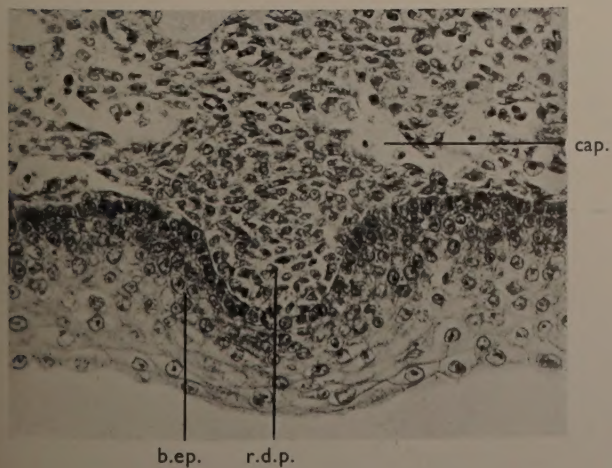


Fig. 46

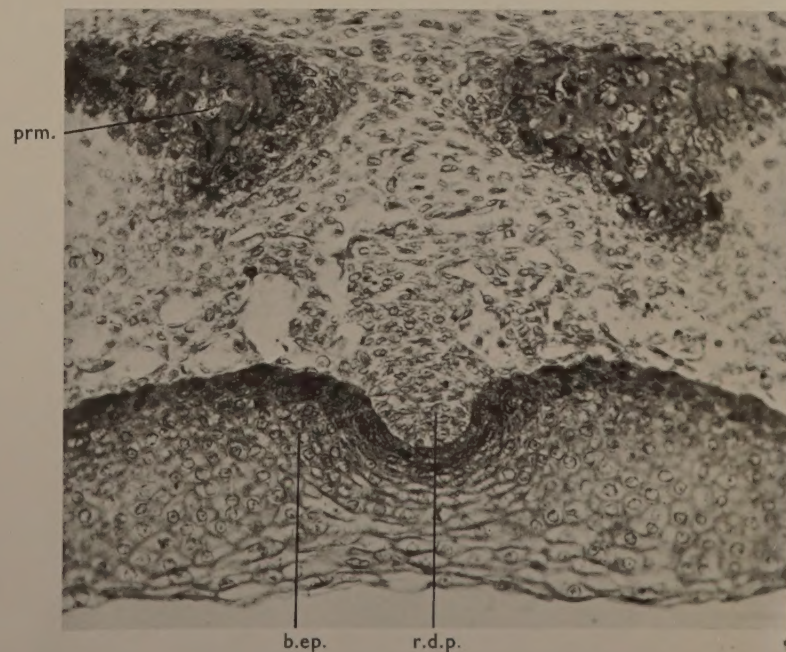
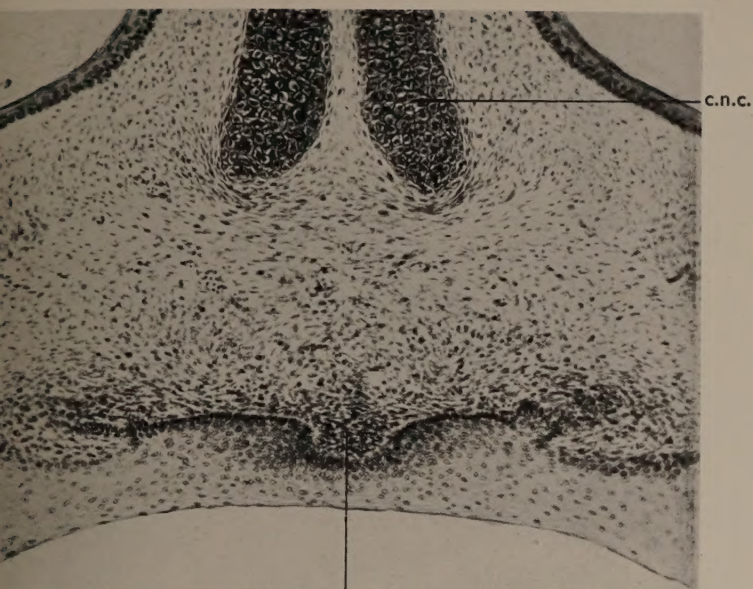


Fig. 47









r.d.p.  
Fig. 48

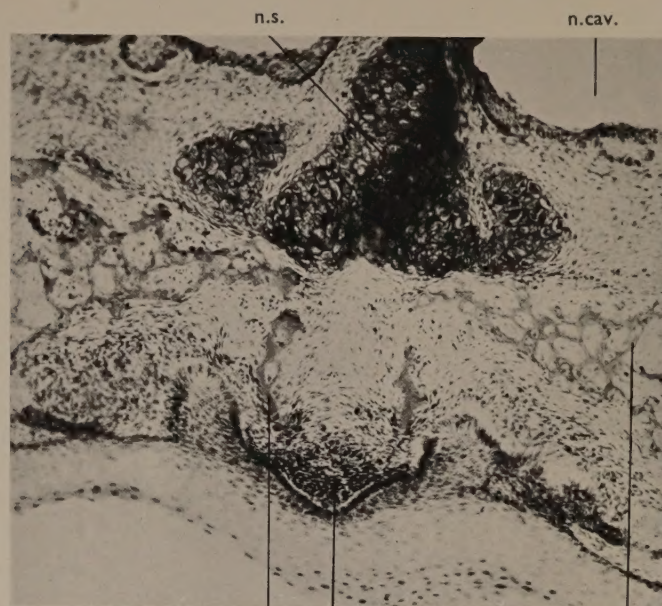


Fig. 49

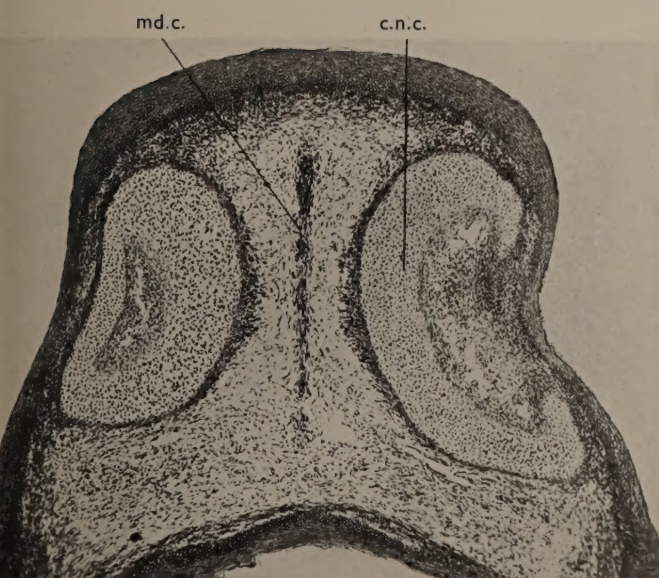


Fig. 50

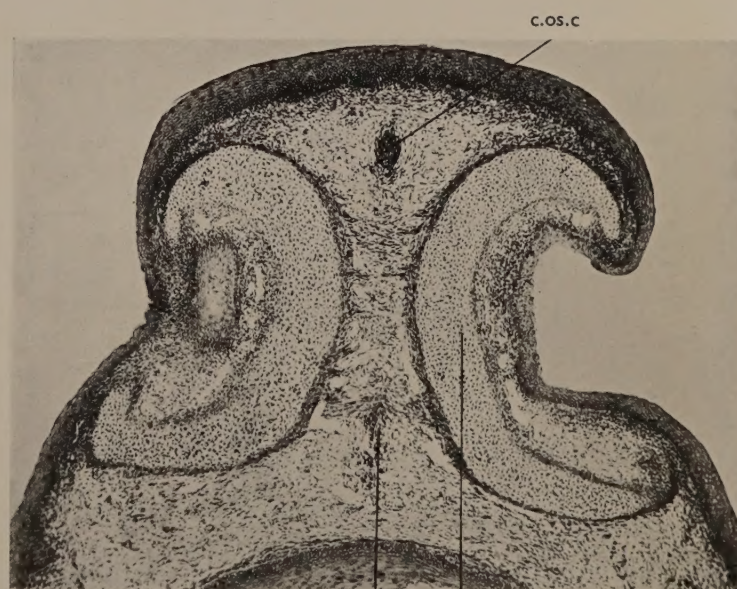


Fig. 51

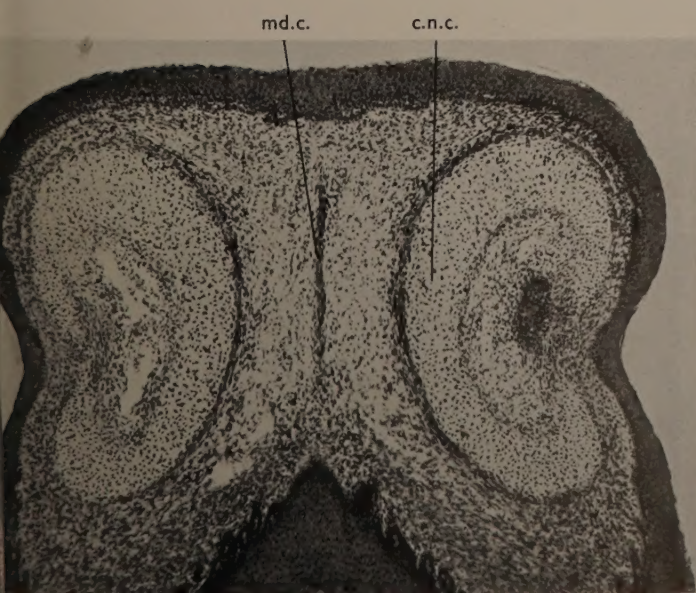


Fig. 52

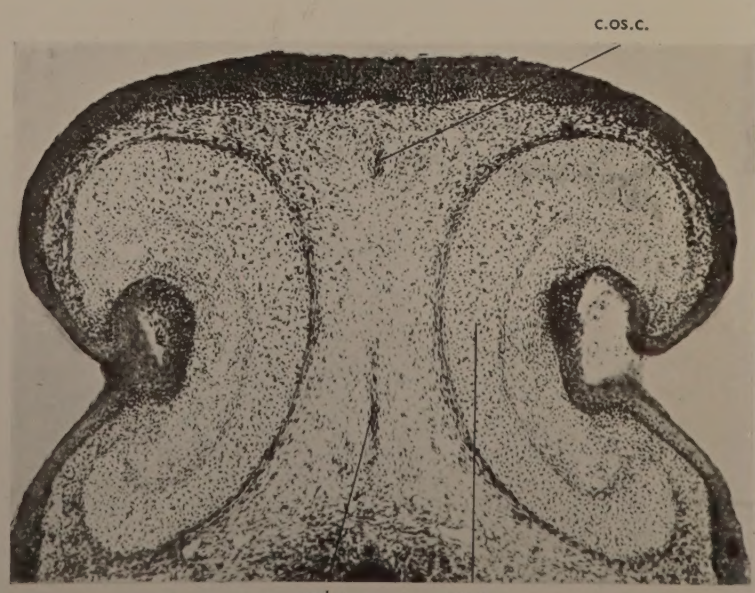


Fig. 53



